Waterfowl Production on the Woodworth Station in South-central North Dakota, 1965-1981

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By Kenneth F. Higgins
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Contents

Foreword

The maintenance of healthy wetland and upland environments and desired populations of waterfowl depends on increasingly sophisticated management programs for public and private lands. Knowledgeable professionals and others must learn to work together to make such programs successful. New management techniques, properly researched and tested, need to be made available to managers and incorporated into broader programs as quickly as possible. These principles were some of the basics incorporated into the initial program of the Northern Prairie Wildlife Research Center when it was established in 1963. My good fortune was to have been involved in the early planning and direction of that program.

One program concept was to have a sizable tract of land in the Missouri Coteau, within 80 km (50 miles) of the Center, for conducting long-term research on habitat change and response by prairie ducks. The area was to be representative of the prairie pothole region, in an area of grasslands and mixed agriculture, with an accessible site for construction of field laboratory facilities, and suitable for demonstration projects. The Woodworth site was selected and it centered around an initial group of waterfowl production areas, eventually enlarged to the present block of 1,070 ha (2,650 acres).

The Woodworth Station's research and management programs evolved rapidly under the able direction of the authors of this publication. They had a special interest in developing new wetland enhancement and upland habitat management techniques that could be applied to broader land use practices and programs, for the purposes of increasing production and survival of prairie ducks, other migratory birds, and resident wildlife. These biologists were also keen on speedily translating research findings to management applications to aid wildlife managers and administrators.

During the first 17 years of the program, the authors were eminently successful in achieving many of the initial research and management objectives described in this publication. The Station developed an international reputation for its work in developing dense nesting cover, maintaining desired native grassland succession through controlled burning, determining optimum frequency for habitat manipulation, identifying the effects of mammalian predation on ground nesting ducks and other birds, and in understanding the relation of wet and dry cycles to waterfowl production and waterfowl nesting in croplands. Other objectives require future emphasis, such as establishing demonstration areas to better acquaint scientists, wildlife managers, agriculturalists, and farmers with land use practices that would maximize benefits to prairie ducks and other wildlife. As with any research program, increasing demands for new investigations were not always matched by additional funds and personnel.

Nevertheless, during the past 28 years, the Woodworth Station has made a significant contribution to waterfowl management, especially in the Prairie Region of the United States and Canada. The scientific publications produced by researchers and managers associated with the station further verifies that contribution. During the period, approximately 300 graduate students and visiting scientists have used the facility. In 1990, the Station also became headquarters for the Chase Lake Project of the Prairie Pothole Joint Venture under the North American Waterfowl Management Plan.

I would especially note that the station program demonstrated the value of long-term studies and systematic monitoring of changes in habitat, climatic conditions, and concurrent responses by prairie ducks and other wildlife populations. This value will become increasingly important during the next 25 to 50 years. It is essential, therefore, that the annual monitoring program and periodic habitat manipulations be continued either by research or management personnel.

The next generation of waterfowl research biologists, wildlife managers and administrators, and those who follow will owe a debt of gratitude to the foresight and capabilities of the authors, and to those who assisted them in carrying out the original mission of the station. I consider it an honor and a pleasure to have been associated with the early team.

Harvey K. Nelson
Executive Director
North American Waterfowl and Wetlands Office
U.S. Fish and Wildlife Service, Washington, D.C.

We dedicate this publication to the memory of

ROBERT (BOB) B. OETTING, PH.D.

To a man of dedication and love for natural resources. To one who could administrate a program and also know its wildlife benefits. To a man of vision and goals, yet one in touch with life's humor and rewards.
And last, to a beloved friend and colleague.

Waterfowl Production on the Woodworth Station in South-central North Dakota, 1965–1981

by

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Abstract. During 17 years of study at the Woodworth, North Dakota study area, the percent of 548 wetland basins with water during 1–15 May ranged from 8 to 87 and averaged 56; waterfowl pair densities varied from 19 to 56/km^2 and averaged 40/km^2. Pond occupancy by duck pairs averaged 37% during mid-May counts and 48% for late May and early June counts. A positive linear relation occurred between the estimated number of duck pairs and the percent of basins with water during 1–15 May.

There were 3,339 duck nests found in grassland habitats from 1966 through 1981. Approximately 66% (85% Mayfield) of these were depredated or abandoned. Mammals caused 88% of nest failures. Half or more of the eventually successful clutches were unhatched by 10 July in 9 of 16 years. Haying would have disturbed or destroyed an average of 43%, 33%, 22%, 15%, and 9% of the duck nests if initiated on 10 July, 15 July, 20 July, 25 July, and 1 August, respectively.

The total average size of completed clutch for all species was 29% smaller at the end of the nesting season than at the beginning, underscoring the importance of protecting early clutches.

Production averaged 30 broods per 100 pairs of ducks and ranged from 15 to 61 broods per 100 pairs. Brood densities ranged from 10 to 63/km^2 and averaged 12/km^2. Mean brood size averaged 6.4 for all species. July broods averaged 7.2 ducklings and August broods 5.7 ducklings. Duckling loss averaged 2.6 per brood and 85% (2.2 ducklings) of this loss was estimated to occur during the first 14 days after hatch.

Wetlands of all sizes and classes were important at some time to one species of duck or another. With the exception of some diving ducks, all species used a complex of sizes and classes of wetlands for space, food, and shelter necessary for nesting and brooding.

Pair counts during 20 May–7 June were most indicative of the breeding population. A combination of two brood counts resulted in the best estimate of annual production. An

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average of only 50% of the total duck broods per year was counted during the 1–15 July surveys, which approximated the average time of the Service's July aerial surveys.
During this study the area produced an average of 1 duck per 4 ha of upland and had a nest density of approximately 1 nest per 14 ha. Nest success rates averaged 35.1% (16.3% Mayfield). Predation was significantly reduced by good vegetative cover at nest sites. Seeded grasslands (dense nesting cover) yielded better production than native prairie or croplands. Seeded grasslands also produced 3 times more ducklings per unit area than adjacent native prairie and more than 14 times as many as adjacent, annually tilled croplands.

Ducks generally showed higher nest densities and better nesting success when using growing grain crops than when nesting in standing or mulched stubble fields. Among native mixed-grass prairie and seeded grassland, production was enhanced by leaving fields idle or by treating them with periodic burning. Duck production was generally lowered by grazing fields of native prairie but duck production on grazing lands was higher than in annually tilled croplands.

Key words: Duck breeding pairs, duck production studies, fire effects, grazing effects, land-use research, nesting habitats, North Dakota, prairie pothole region, waterfowl recruitment indices, wetlands research .

Each spring, millions of ducks migrate northward from wintering areas to nest in and near wetlands of the prairies, parklands, and woodlands of the north-central United States and south-central Canada. The reproductive success or failure of these duck populations is largely determined during spring and summer. An understanding of factors that affect the success or failure of nests is essential to duck management.

The Woodworth Field Station (WFS) of the Northern Prairie Wildlife Research Center (NPWRC) was initially purchased as a Waterfowl Production Area with duck stamp dollars. Station field investigations began in April 1963 and included a historical land ownership survey, mapping of the vegetation, cultural features, land use, and wetlands, and a survey of wildlife (Bayha 1963, 1964). Results of the 1963 and 1964 investigations are unpublished but are on file at NPWRC in Jamestown. The study area was expanded in 1964 to include all WFS lands subject to later purchase by the U.S. Fish and Wildlife Service (FWS); consequently, for 1963, only historical or land-use data are included in this report.

From 1964 through 1968, land-use treatments on the study area were maintained similar to those of prior years when the land was in private ownership. Since 1969, the station has been used for studying the response of wildlife to applied treatments of grazing, burning, idling, and annual cropping.

Even though our research did not address the effects of hunter harvest on local duck populations, we were aware of many changes in hunting styles and equipment through the years. For example, since 1964 hunters have had easier and greater access to fields and wetlands because of increased technology and off-road, primarily four-wheel drive, vehicles. Many hunters also used campers or established semipermanent housing on or near hunting areas, thus, increasing a persistent, and often intensive, hunting pressure on specific wetlands and public areas.

Long-term ecological studies of waterfowl production in the glaciated prairie pothole region of north central North America (Kiel et al. 1972; Smith 1971; Stoudt 1971, 1982; Leitch and Kaminski 1985; M. C. Hammond, unpublished data) have been relatively few in comparison to hundreds of short-term (<10 years) studies. With the exception of our study and the early waterfowl studies of M. C. Hammond, all other long-term waterfowl studies were conducted in Canada, mostly in the Aspen Parklands (Bird 1961) of the Prairie Provinces. Trauger and Stoudt (1978), Bellrose (1979), and Hammond and Johnson (1984) completed more recent reviews and analyses of some of these earlier long-term studies and

associated data sets. The studies at the WFS were designed to address wildlife responses to land management changes (Miller 1971) and to evaluate their relevance to past and future management of these and other lands dedicated to wildlife production.

Scientific and common names of plants were taken from Stevens (1963); birds—Appendix B—and mammals—Appendix C—from Banks et al. (1987); reptiles and amphibians—Appendix D—from Collins et al. (1982); and fish—also Appendix D—from Robins et al. (1980).

Study Area

The Woodworth Study Area (WSA) is located in northwestern Stutsman County about 5 km east of Woodworth, North Dakota, and about 56 km northwest of Jamestown, North Dakota (Fig. 1). Altitude above sea level ranges from 561 m on the east to 594 m on the west and north. The study area is a large block of continuous habitat and is nearly 4 km^2. It contains about 1,231 ha (3,040 acres), of which 1,073 ha (2,650 acres) are federally owned (Fig. 2). A summation of the physical characteristics of the WSA appears in Table 1.

The WSA is on the Missouri Coteau (Winters 1963), a biogeographic region extending from east central South Dakota through North Dakota into southwestern Saskatchewan, a distance of about 1,287 km. The Coteau is an area of morainic hills averaging 48 km wide. In North Dakota, the Coteau covers 25,584 km^2 and the northeast-facing escarpment rises 91–152 m above the adjacent Drift Plain. Unlike the slightly rolling, intensively farmed land to the east, the Coteau has irregular terrain with an interspersion of wetlands, native prairie pastures, hayfields, and a variety of grain crops. This large contiguous Coteau is of major importance to North American waterfowl (Stewart and Kantrud 1973).

The Coteau consists primarily of dead-ice moraine left from extensive glacial stagnation that followed advances of late Wisconsin glaciers. Most of the glacial drift on the Coteau has been aged at 9,000–13,000 years (Tuthill et al. 1964; Clayton 1966; McAndrews et al. 1967).

The WSA has two major glacial landforms (Winters 1963): hummocky stagnation moraine and outwash (Fig. 3). The hummocky stagnation moraine is rugged with an average altitude more than 564 m above sea level, consisting mainly of knobs and kettles. Dominant material is till. Linear patterns associated with end moraines are not apparent. Local relief sometimes exceeds 30 m/km^2 of land. Stagnation outwashes are extensive areas underlain by glaciofluvial material deposited in association with stagnating or dead ice. As a result of stagnation, the glacier disintegrated in place, causing the rugged glacial topography of the area, and the closely spaced hills and

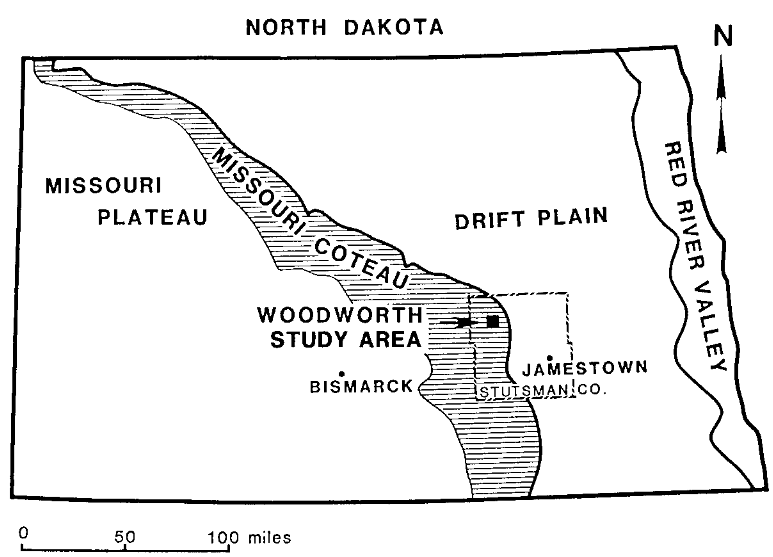

Fig. 1. Location, Woodworth Study Area, North Dakota.

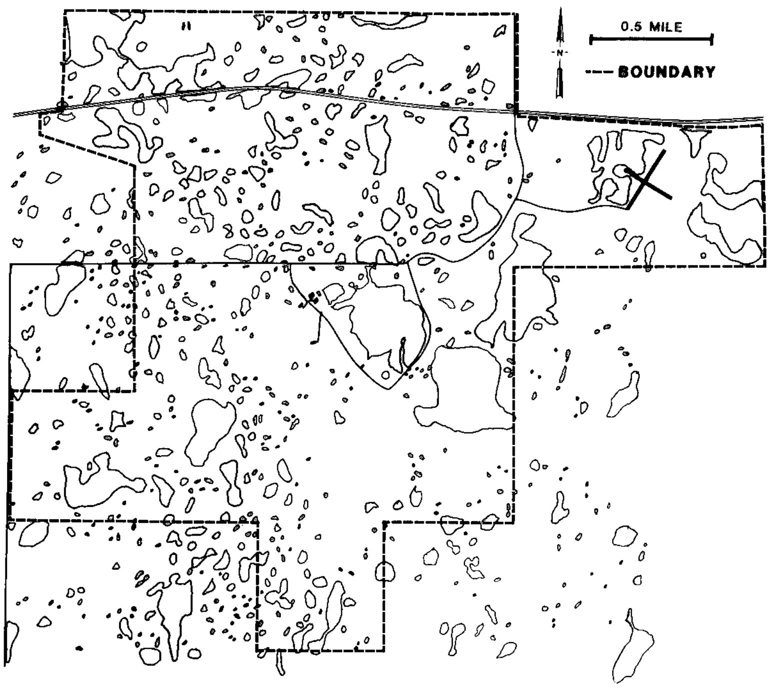

Fig. 2. Wetlands distribution, Woodworth Study Area.

Table 1. *Physical characteristics of the Woodworth Study Area.*

Location	5 km (3 miles) east of Woodworth, N.Dak.
Latitude and longitude	47° 8′ N - 99° 15′ W Elevation 572 m (1,877 feet) ASL
Geographic location	Northern Great Plains prairie pothole region
Biogeographic province	Missouri Coteau
Topography	Stagnation moraine, knob and kettle
Study area size	12.3 km^2 (4.75 square miles), 1,231 ha (3,040 acres)
Number of wetland basins	548
Total area in wetlands	235.88 ha (582.42 acres)
Percent in wetlands	19%
Percent in croplands	30%
Percent in miscellaneous	3%
Percent in native grass	48%
Area in shelterbelts, roads,pens, rights-of-way, and headquarters	42.16 ha (104.10 acres)
Density of wetland basins	72 per square kilometer (28 per square mile)
Mean basin area	0.43 ha (1.06 acres)
Area in native grasslands	587.85 ha (1,451.48 acres)
Area in croplands	365.31 ha (902.0 acres)
Soil parent materials	Glacial till
Soil primary association	Buse–Barnes
Potential natural vegetation	Habitat: *Agropyron–Stipa*
Climatic region	Cool temperate subhumid
Long-term average annual precipitation	43.69 cm (17.0 inches)
Long-term average annual snowfall	86.36 cm (33.7 inches)
Long-term average annual frost-free period	120 days
Long-term average date of last 2.5 cm of snow cover	25 March
Long-term mean annual temperature	4° C (40° F)
Average depth of frost penetration	1.5 m (4.9 feet)

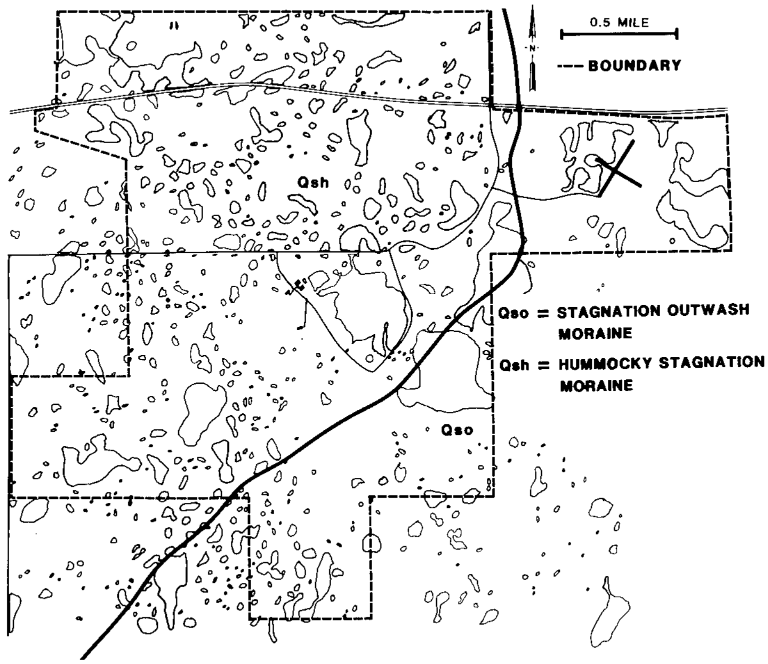

Fig. 3. Primary glacial landforms, Woodworth Study Area.

depressions. Many of the depressions contain wetlands of various sizes, shapes, and depths, often called potholes. Superimposed and collapsed outwash is included in this unit. This landform contains an ice-restricted gravel train discussed by Winters (1963).

The greatest number of potholes on the area occurs in the hummocky stagnation moraine and may exceed 40 basins per square kilometer of land. The stagnation outwash landscape has fewer pothole basins, but some of them are quite permanent because aquifers contained in the gravel train provide a high water table, seepage, and springs.

Parent materials of the soils of the area were deposited by glacial ice and are classified as glacial till. Glacial till is a random mixture of sand, silt, clay, pebbles, and stones with no sorting of the various-sized particles. The clay-sized fraction is dominantly montmorillonite (Omodt et al. 1968; Fig. 4).

The major soil association of the area is Buse-Barnes (Omodt et al. 1968; Patterson et al. 1968). This association occurs on hilly to rolling and undulating topography with pothole depressions common between hills, knobs, and ridges. This association has no major stream drainage. Surface runoff flows into many pothole depressions that are usually inundated for several weeks or longer in spring and summer.

Svea, Renshaw, Fordville, Sioux, Parnell, Colvin, and Tetonka soils also occur in this association. Svea soils occur on the concave side slopes and foot slopes of the knolls and hills. Renshaw, Fordville, and Sioux soils occur on small areas of outwash. Renshaw soils are moderately deep and Sioux soils are shallow over a gravel substratum. Parnell, Colvin, and Tetonka are the main soils found in wetland basins on the area.

Some predictive equations of soil moisture seem more related to wetland performance than 12-month precipitation amounts (Boyd 1981). Following Williams and Robertson (1965), conserved soil moisture was estimated in early May each year from the equation:

$$M = 0.36A + [0.37B - 0.2\,(0.36A)] + 0.13C + \{0.30D - 0.2[0.36A + (0.37B - 0.2(0.36A)) + 0.13C]\},$$

where

A = total precipitation during fall of the summer fallow period (August, September, and October in year t-2),

B = total precipitation during the first winter of the summer fallow period (November, t-2, to April, t-1),

C = total precipitation during the summer of the summer fallow period (May to October, t-1),

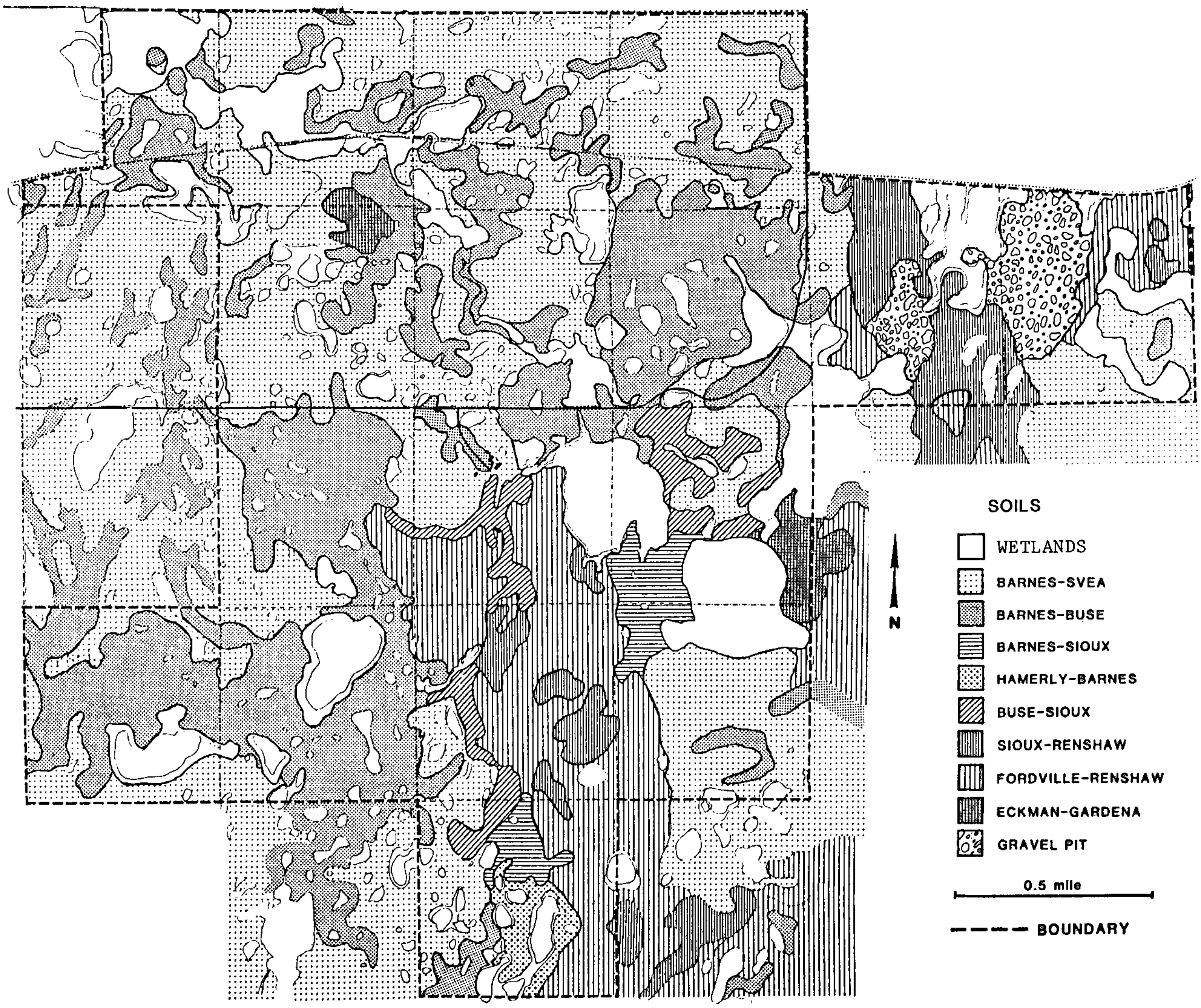

Fig. 4. Soil associations, federally owned lands, Woodworth Study Area.

D = total precipitation during the second winter (November, t-1, to April, t).

The continental climate of the WSA is characteristic of much of the northern Great Plains, having a low precipitation–high evaporation ratio and cold winters–warm summers. The average number of clear days between sunrise and sunset is 112 per year. Average depth of frost penetration is 1.5 m and the extreme is 2 m (Bavendick 1952). Average relative humidity is 68%. Several studies have shown that for the past few hundred years, the northern grasslands have occupied their present areas with rather arid weather conditions (Will 1946; Dix 1964; McAndrews et al. 1967; Shay 1967; Wells 1970).

Precipitation records for the study area were taken in the town of Woodworth before 1966 and on the WSA since 1966 (Appendix A). During the study, total annual precipitation varied from a low of 23 cm in 1967 to a high of 58 cm in 1965. Mean annual precipitation for the years 1964–81 was 41 cm and the long-term (>50 years) mean annual for the vicinity was 44 cm (Bavendick 1952; Jensen 1972; Table 2). Precipitation is least and nearly always in the form of snow during winter. The first substantial rains of spring usually occur in early April, but sometimes in late March. Precipitation

Table 2. *Long-term mean precipitation and temperature, Woodworth Study Area.*

Month	Mean precipitation cm	Mean precipitation inch	Mean temperature °C	Mean temperature °F
January	1	0.4	-14	7
February	1	0.4	-12	10
March	2	0.8	-5	23
April	3	1.2	4	40
May	6	2.3	12	54
June	9	3.5	17	63
July	7	2.7	21	70
August	6	2.3	20	68
September	4	1.6	14	57
October	3	1.2	7	45
November	2	0.8	-3	26
December	1	0.4	-10	14
Annual	44	17.2	4	40
April–September	34	13.3	15	59
October–March	10	4.0	-6	21

is greatest during summer, usually peaking in June.

Precipitation amounts decrease rapidly throughout the fall, and the first significant snowfall usually occurs in late November. Average mean annual snowfall is 86 cm for the study area. Mean date of first 2.5 cm or more of snow depth is 5 December and the mean date of last 2.5 cm of snow cover in spring is 25 March.

Mean annual temperature for the vicinity is 4° C (Bavendick 1952; Jensen 1972). January is the coldest month and July is the warmest (Table 2). The extreme high temperature for the vicinity during the study was 48° C and the extreme low -58° C. Mean length of freeze-free days is 120 and usually occurs between 20 May and 15 September.

Local topography of the area affects temperature in two ways. First, the WSA, on the eastern edge of the Missouri Coteau, is higher than surrounding physiographic regions. Temperatures on the WSA are usually from 1 to 3° C colder for this reason. Second, colder air accumulates in pothole depressions, often causing temperatures there to be several degrees colder than nearby uplands.

The prevailing wind flow is from the northwest with an average daily speed of 16 km/h. Winds are usually sustained strong breezes rather than occasional gales. Wind speeds are usually highest during the afternoon and lowest at night. At wetland sites, winds of 40–48 km/h often last for 6 h and have been known to last for as long as 15 h. Winds of more than 48 km/h have been observed to last longer than 6 h (Eisenlohr et al. 1972). Wind is an important factor affecting evapotranspiration rates on wetlands as well as on uplands.

Wetland Water Budget

Eisenlohr and Sloan (1968), Shjeflo (1968), Eisenlohr et al. (1972), Sloan (1972), and Winter and Carr (1980) present descriptions and discussions of factors influencing wetland (pothole) water budgets in this area. Reference lists supplement these presentations. The following summary of a generalized pothole water budget was compiled from these papers, many of which were based on data gathered on or near the WSA.

Sources of water for a pothole are precipitation on its surface, overland flow or runoff, and underground or seepage inflow.

Rainfall on wetlands and their basins is the greatest direct addition of water in the WSA. The net amount of direct winter precipitation varies from pothole to pothole because of wind transportation of snow. Potholes with tall, emergent vegetation tend to accumulate drifting snow.

Snowmelt water flowing over frozen ground is probably the largest source of runoff water to prairie potholes because runoff adds to pothole water only when water can flow over the ground without being absorbed; the ground must be either frozen or saturated. Size of the watershed into a basin also affects the amount of runoff to pothole basins.

Seepage inflow of groundwater depends on configuration of the adjacent water table and hydraulic conductivity of the glacial drift. Movement of groundwater to and from potholes in glacial till is relatively slow but is significant because it increases or decreases the rate of water loss and water levels in potholes. Winter and Carr (1980) showed that a complex interrelation seems to occur

between wetlands and groundwater. In their study, some wetlands seemed to recharge groundwater, some were flow-through types where groundwater enters one side and surface water seeps into the ground on the other side, and some were discharge points for groundwater. They also found that water flowage in or out of wetlands varied throughout the year.

Natural loss of water from potholes occurs by transpired evaporation, surface overflow, and seepage outflow of groundwater. Water loss also results from drainage, seepage to irrigation wells, and pumping and siphoning.

Evapotranspiration of water directly from potholes is generally the cause of most water loss. Average seasonal evapotranspiration losses for both clear and vegetated potholes was found to be about 0.6 m for the season May–October (Shjeflo 1968). Presence of emergent aquatic vegetation increases the evapotranspiration rate. Average annual lake evaporation for the area is about 81 cm (Kohler et al. 1959) and occurs during the ice-free period, April–September. Evaporation is greatest from potholes free of emergent vegetation (Eisenlohr and Sloan 1968).

Seepage outflow of groundwater, like groundwater inflow, depends on configuration of the adjacent water table and hydraulic conductivity of the glacial drift.

Overflow loss of pothole water occurs when the water supply exceeds the pothole basin holding capacity. Overflow loss of water is usually relative to an individual pothole because other potholes lower in the watershed may absorb the overflow from higher basins. Much of the water supply to bigger potholes is dependent on overflow water from smaller potholes. Such overflow is usually of short duration for most potholes, and many large basin potholes do not overflow. Frequency of overflow is related to the amount of precipitation and spring runoff.

Waterfowl and Predators

Twelve species of ducks commonly nested on the WSA: mallards (*Anas platyrhynchos*), gadwalls (*A. strepera*), American wigeon (*A. americana*), green-winged teal (*A. crecca*), blue-winged teal (*A. discors*), northern shovelers (*A. clypeata*), northern pintails (*A. acuta*), redheads (*Aythya americana*), canvasbacks (*A. valisineria*), lesser scaup (*A. affinis*), ring-necked ducks (*A. collaris*), and ruddy ducks (*Oxyura jamaicensis*). Canada geese (*Branta canadensis*) were released on the area in 1966 and wood ducks (*Aix sponsa*) in 1969 (Doty 1974); some of each species still nest there. Only rarely did an American black duck (*Anas rubripes*) or cinnamon teal (*A. cyanoptera*) remain during the nesting season (Klett and Lokemoen 1968). These and other bird species that occur on the WSA during breeding season are listed in Appendix B.

Mammals common to the study area are listed in Appendix C. Coyotes (*Canis latrans*) had been absent from the area since the mid-1950's until 1973. Two were seen on the study area on 13 February 1978 and one male was trapped on the study area in 1979. Coyotes returned to the Woodworth vicinity primarily because use of aerial gunning and 1080 poison control measures was reduced. Red fox (*Vulpes vulpes*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), badgers (*Taxidea taxus*), and mink (*Mustela vison*) were common throughout the study. Long-tailed (*Mustela frenata*) and least weasels (*M. nivalis*) were seen infrequently on the area and their abundance changed only slightly with changes in small rodent populations (Lokemoen and Higgins 1972). Weasels were locally abundant in the 1940's and 1950's. Their presently reduced status is believed due to red fox predation and land-use changes.

Three species of ground squirrels were present at all times. Before 1969, Richardson's ground squirrels (*Spermophilus richardsonii*) were the most abundant. Since 1969, thirteen-lined ground squirrels (*S. tridecemlineatus*) have been the most abundant, probably due to the establishment of taller, denser cover on former croplands. Thirteen-lined and Franklin's ground squirrels (*S. franklinii*) associated with taller and denser vegetation sites whereas Richardson's ground squirrels more often occurred with short and sparse vegetation and grassland pastures, especially overgrazed areas.

Native Grasslands

The WSA is in the Mixed-prairie Grassland region of North Dakota (Weaver and Clements

1938; Clements and Shelford 1939), about 150 km west of the True Prairie Grassland region and about 250 km south of the Aspen Parkland region of southern Canada (Bird 1961). Küchler (1964) termed this area a wheatgrass–needlegrass (*Agropyron–Stipa*) grassland of moderately dense, short or medium-tall grasses. Whitman (1963) denoted the area as a transitional zone between the eastern tall-grass prairie and the western short-grass prairie in North Dakota. Dix and Smeins (1967) also recognized that the central part of the state was in the transitional belt of mixed-grass prairie vegetation; they described the general phytosociological structure of the native prairies, meadows, and marshes in a transitional area in Nelson County and related it to the True and Mixed prairies. Stewart (1975) presented a list of the predominant plants of the eastern mixed-grass prairie of North Dakota and included the Missouri Coteau as part of that region. General descriptions of vegetation on the study area have been made by Kirsch (1969), Johnson and Springer (1972), Higgins and Kirsch (1975), Kirsch and Higgins (1976) and Meyer (1985).

Native grasslands (Fig. 5) on the WSA constitute typical xeric mixed-grass prairie. Because of the hummocky topography, most of the vegetation of similar nature is either in patches, clones, or thickets. The largest tracts of any one plant community are usually on uniform soil zones with little slope. Complex vegetation zonation occurs throughout the study area and several different

Fig. 5. Native grassland, Woodworth Study Area.

communities may be present along one slope with only slight changes in soils, topography, moisture, or drainage regimes. The most obvious vegetative zonation occurs between brush clumps or thickets, marshes, and grass–forb associations. One prevalent zone is around the edges of wolfberry (Symphoricarpos occidentalis) thickets (Fig. 5). Other common shrubs on the area are silverberry (*Elaeagnus comutata*), prairie wild rose (*Rosa arkansana*), thornapple (*Crataegus chrysocarpa*), chokecherry (*Prunus virginiana*), Juneberry (*Amelanchier alnifolia*), wild black currant (*Ribes americanum*), and willow (*Salix* spp.).

The only trees common to the area are cottonwoods (*Populus deltoides*). Occasionally, single trees of green ash (*Fraxinus pennsylvanica*), hackberry (*Celtis occidentalis*), or Siberian elm (*Ulmus pumila*) occur on prairie sites. The only other trees are those planted in tree groves or shelterbelts.

Dix and Smeins (1967) recognized relative positions of vegetational units by topographic relief or landscape within the transitional mixed-grass prairie belt in North Dakota. Uplands were divided into high prairie, mid-prairie, and low prairie, and lowlands into meadow and marsh. Because Woodworth lies within this same vegetational belt, we have used their terminology to describe the aspect of prairie on the study area (Fig. 6).

High prairie grassland sites are usually on excessively drained Sioux, Fordville, or Buse soils that are shallow, gravelly regosols. Brush species, except for *Rosa*, are nearly always absent. Grass stands are usually dominated by various combinations of blue grama (*Bouteloua gracilis*), needle and thread (*Stipa comata*), fringed sage (*Artemisia frigida*), narrow-leaved blazing star (*Liatris punctata*), prairie wild rose, hairy golden aster (*Chrysopsis villosa*), pasque-flower (*Anemone patens*), threadleaved sedge (*Carex filifolia*), and Missouri goldenrod (*Solidago missouriensis*).

Mid-prairie grassland sites are usually on level to slightly or moderately sloping terrain with Barnes soils that are well drained chernozems. Stands on these sites are dominated by various combinations of green needlegrass (*Stipa viridula*), Kentucky bluegrass (*Poa pratensis*), needle and thread, western wheatgrass (*Agropyron smithii*), wolfberry, northern bedstraw (*Galium boreale*), chickweed (*Cerastium arvense*), white sage (*Artemisia ludoviciana*), yellow sedge (*Carex pennsylvanica*), stiff sunflower (*Helianthus rigidus*), and silver-leaf scurf pea (*Psoralea argophylla*). The mid-prairie sites are vegetationally the most complex communities on the area.

Low prairie grassland sites are on moderately drained chernozem soils. Dominant species include big bluestem (*Andropogon gerardi*), little bluestem (*A. scoparius*), Baltic rush (*Juncus balticus*), cordgrass (*Spartina pectinata*), switchgrass (*Panicum virgatum*), blackeyed Susan (*Rudbeckia hirsuta*), and Maximilian's sunflower (*Helianthus maximiliani*). Less dominant species of these sites are smooth aster (*Aster simplex*), prairie dropseed (*Sporobolus heterolepis*), wild licorice (*Glycyrrhiza lepidota*), and Canada anemone (*Anemone canadensis*).

Lowland meadow grassland sites are poorly drained and the water table is usually within the rooting depths of most plants. Gravitational water is usually present in the marsh sites, and in these depressions or potholes, soils are usually inundated for extended periods. Detailed descriptions of the vegetation of meadow and marsh sites have been reported by Stewart and Kantrud (1969, 1971); only the major dominants are presented

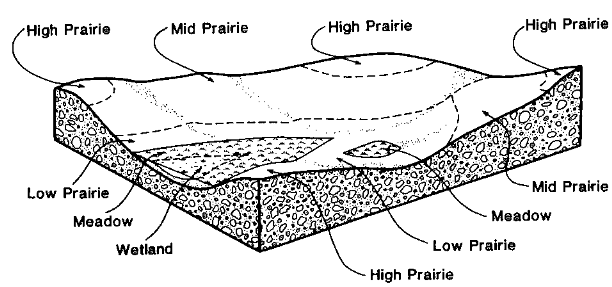

Fig. 6. Schematic of landscape topography showing positions of high prairie, mid prairie, low prairie, wet meadow, and wetlands, Woodworth Study Area.

here. These sites are usually on Colvin, Parnell, or Tetonka soils.

Dominant species of meadows on the area are northern reedgrass (*Calamagrostis inexpansa*), narrow-leafed sedge (*Carex lanuginosa*), foxtail barley (*Hordeum jubatum*), cordgrass, Baltic rush, smooth aster, wild mint (*Mentha arvensis*), fowl bluegrass (*Poa palustris*), and hedge nettle (*Stachys palustris*).

Dominant species of the marshes at the WSA are slough sedge (*Carex atherodes*), whitetop (*Scolochloa festucacea*), common cattail (*Typha latifolia*), hybrid cattail (*T. glauca*), hardstem bulrush (*Scirpus acutus*), slender bulrush (*S. heterochaetus*), softstem bulrush (*S. validus*), spikerush (*Eleocharis palustris*), common smartweed (*Polygonum coccineum*), sloughgrass (*Beckmannia syzigachne*), water-plantain (*Alisma triviale*), bur-reed (*Sparganium eurycarpum*), water parsnip (*Sium suave*), and tall mannagrass (*Glyceria grandis*).

Tilled Croplands

Durum and hard red spring wheat were the main crops seeded on the area; others were barley, winter rye, oats, flax, corn, sunflowers, and speltz. Summer fallow (mostly bare soil) was part of the annual cropping program.

Before 1965, smooth bromegrass (*Bromus inermis*) and alfalfa (*Medicago sativa*) were the main perennials seeded for forage crops. Since 1965, several mixtures of perennial grasses and legumes were seeded on cropland. Yellow sweetclover (*Melilotus officinalis*) was also included in these mixtures but was usually dominant only during the second growing season. Perennial mixtures included various combinations of alfalfa, intermediate wheatgrass (*Agropyron intermedium*), and tall wheatgrass (*A. elongatum*). Crested wheatgrass (*A. cristatum*) was accidentally included in one stand of cover. Another stand had slender wheatgrass (*A. caninum*) and green needlegrass. The predominant mixture seeded since 1968 has included 1 part yellow sweetclover, 1 part alfalfa, 4 parts intermediate wheatgrass, and 4 parts tall wheatgrass for a total of 11.2 kg/ha.

Upland habitats were delineated into continuous field units with designated area, length, and width. Primary upland habitats were classified as croplands, seeded grasslands, or native grasslands (Fig. 7). In this paper, croplands refers to fields that undergo annual tillage or cultivation including barren-soil summer fallow, small grain, oil seed, and row crops, and post-harvest stubble residue left either standing or mulched by discing or plowing. Seeded grasslands refers to fields planted to various mixtures of perennial grasses and legumes that did not require annual tillage. Native grasslands refers to fields of native prairie sod with no tillage history and also to a few small areas with a former cropland history which, through the years, had successionally changed back to native prairie. Generally, native grasslands were partially invaded to various degrees by Kentucky bluegrass, smooth bromegrass, and quackgrass and included scattered stands of native brush and shrubs, mainly wolfberry, silverberry, and chokecherry.

Land Use Treatments

There were seven basic land-use treatments applied to three habitat types. Treatments for annually tilled cropland habitat included standing crop, standing stubble, mulched stubble, and summer fallow. Treatments for either native mixed-grass prairie or seeded grasslands included grazing, prescribed burning, and idling or nonuse.

In this paper, grazed refers to habitats subjected to a month or more of livestock grazing at some time during the year. Grazing usually occurred between April and November for various lengths of time. Burned refers to habitats subjected to a rotation of periodic prescribed fires with intervals of nonuse between fires. For example, a field burned in 1971, rested during 1972–74, and burned again in 1975 was referred to as burned for the entire period 1971–75. A major problem with published fire and duck nest success data is the lack of a term for an area that is no longer being burned and is going into nonuse; thus, the reason for our definition of burned. Idle refers to habitats that were not grazed by livestock, burned, or tilled for usually more than 5 years in succession. These habitats were open to use by native wildlife and, except for an occasional trail, there were no visually obvious wildlife use effects.

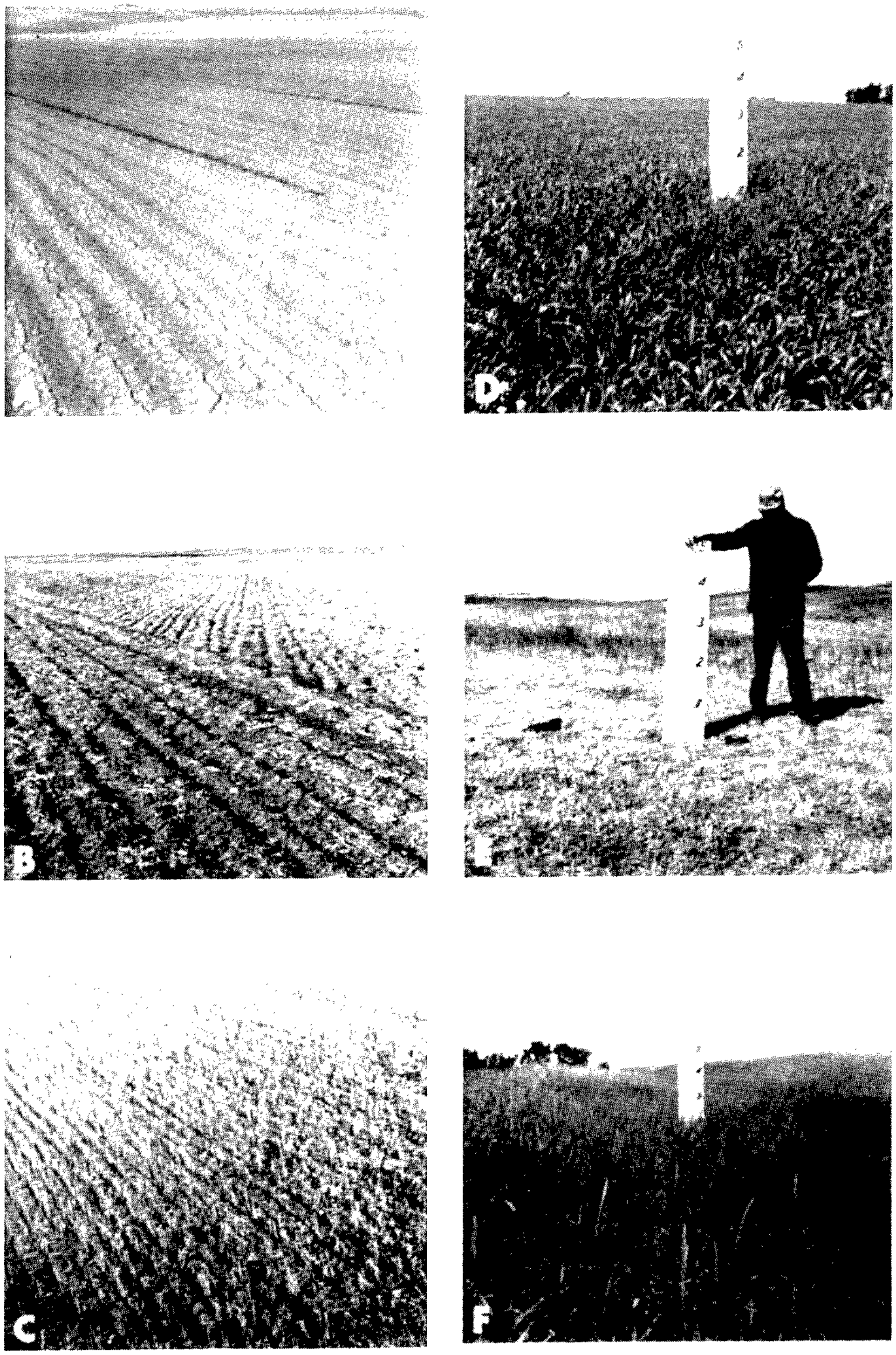

Fig. 7. Photographic summary of main types of land-use treatments and habitats, Woodworth Study Area: A = summer fallow, B = mulched grain stubble, C = standing grain stubble, D = growing grain, E = native prairie, and F = seeded grassland.

Height, density, and rankness were recognized as important vegetative characteristics of quality nesting cover. We used poor, fair, good, and excellent as a subjective method of rating the quality (Kirsch and Higgins 1976) of cover surrounding each nest. Poor cover included bare summer fallow fields, overgrazed pastures, feedlots, mulched stubble fields, mowed areas with little or no regrowth, and brush clumps with no understory vegetation. Most cover was 15 cm or less in height. Such areas provided little nesting material and probably no barrier to predator movements. Fair cover included fields of standing stubble, moderately grazed pastures, mowed areas with heavy regrowth, brush clumps with some understory vegetation, and vegetation on poor soils. Most cover averaged 15–30 cm in height. Such areas provided thin, uniform nesting cover or scattered clumps of fairly dense cover but little barrier to predator movement. Good cover included lightly grazed pastures, undisturbed vegetation on some sites, and brushy clumps with grassy understory. Such areas provided large expanses of nesting cover with only occasional openings or paths, and offered a moderate deterrent to predator movements. Excellent cover included stands of tallgrass or grass–forb mixtures on good soils. Most cover was taller than 60 cm. Such areas provided heavy cover with no paths, roads, or trails and only scattered small openings, and possibly offered a barrier to some mammalian predator movement.

Wetlands

Wetlands on the study area were classified almost annually during July–September according to Stewart and Kantrud (1971). Five natural and nine disturbed classes of wetlands occurred on the study area. Natural wetlands included Class I, ephemeral potholes; Class II, temporary potholes; Class III, seasonal potholes; Class IV, semipermanent potholes; and Class V, permanent potholes.

Classes of disturbed wetlands included those tillaged and human-made. Classes of wetlands altered by tillage and usually located in cropland fields or fields seeded to tame grasses and legumes included Class I^t, tilled ephemeral; Class II^t, tilled temporary; and Class III^t, tilled seasonal. The superscript t identifies that the natural classes of these ponds can be recognized, but that 50% or more of the central zone of the wetland basin was occupied by emergent plant associations characteristic of tilled conditions. Other artificial classes in tilled wetlands included T-4 summer fallow (bare soil), T-3 mulched stubble, and T-2 standing stubble. For these ponds, a capitol letter T was substituted for the class number because the natural class could no longer be recognized. The names such as mulched stubble describe the vegetation.

Human-made water areas included dugouts, stock water dams, and recreational impoundments. The dugouts were deep excavations, 15 × 30 m or less, located in drainages or seepages. Stock water dams were dirt dams constructed across natural drainage ditches. Neither dugouts nor stock water dams inundated natural wetland basins. Recreational impoundments included natural wetlands with human-made dirt dams constructed on the natural overflow drainages from wetland basins. During years of high runoff, these dams caused higher water levels in the existing natural wetland basins; during dry years, the wetlands were, in a sense, natural.

All wetlands on the study area were Subclass A (fresh) to B (slightly brackish) ponds (Stewart and Kantrud 1971). These were combined because plant species characteristic of relatively fresh water predominated. Average salinity differences for fresh to slightly brackish surface waters are classified by Stewart and Kantrud (1971) according to normal and extreme ranges of specific conductance (micromhos per cubic centimeter). Indicators of differences in average salinity are: fresh, normal (<40–500) and extreme (<40–700); slightly brackish, normal (500–2,000) and extreme (300–2,200). The lowest and highest specific conductance readings in wetlands on the study area were 470 and 1,650 μmhos/cm^3, respectively.

Methods

Annual field investigations usually included notation of bird arrival dates, surveys of early spring residual vegetation, wetland water censuses, duck pair and brood counts, nest searches,

land-use inventories, wetland classification surveys, and late summer vegetation surveys.

Wetlands were classified as wet when a basin was at least 5% inundated and the water was 2.5 cm or more deep. Five water surveys were usually made annually; one soon after all snow and ice had melted from the uplands and wetlands, and four during duck pair and brood counts. For purposes of analyses, water surveys were grouped into five periods: 1–15 May, 1–15 June, 16–30 June, 1–15 July, and 1–15 August.

Counts of breeding pairs (Hammond 1969) of adult ducks (hereinafter called pairs) were made to provide indexes to the number of pairs nesting on the study area. Between 10 April and 10 July, eight pair counts were made in 1964; six in 1965–67 and 1969; five in 1968; three in 1970–71; and two in 1972–81. An evaluation of the pair counts from 1964 to 1969 indicated that pairs could be estimated as well based on data from two counts as from three or more counts. The time period with relatively stable duck numbers was usually between 25 April and 15 June.

Counts were made while walking, driving a motorbike, or driving a jeep around the periphery of wetlands. On larger wetlands and lakes or on wetlands choked with emergent vegetation, two people started counting ducks from a point on the shoreline and walked or waded in opposite directions until they met. On such counts, notes were compared to eliminate duplication. One person could count ducks on small wetlands. If ducks were flushed from wetlands during the count, their flight pattern or descent to another wetland was noted to avoid duplicate counting of the same ducks on wetlands scheduled to be counted. Ducks passing over in flight but not flushed by a counter were not included in the census.

During pair counts, all ducks were identified by species and sex within each group and recorded on field maps. The decision to segregate or aggregate duck populations on wetlands was made as follows: several ducks close to each other were considered one group; several ducks, either in singles or aggregates, spaced distantly from each other were considered several groups; and a single duck was considered a group. Final tabulation of pairs was made according to Hammond (1969): all waterfowl and other groups and flocks were recorded except those flying over the sample or transect and those flying into the sample area and landing. Indicated pairs were partitioned for final tabulation: segregated pairs and lone drakes were tabulated for both dabbling and diving ducks, lone hens were tabulated only for diving ducks and only when males were not nearby, and male groups and mixed groups of males and females were tabulated for groups up to five with the exception of northern shovelers and American wigeon for which only lone males and pairs are counted (Hammond 1969).

The time required to complete a pair count on the study area depended on the number and size of wetlands to be counted, number of people available, amount of emergent vegetation in wetlands, weather conditions (especially wind, heat, and rain), and number of ducks. During wet years, when many ducks were present, 3–4 days were required per count, and during dry years, when smaller numbers occurred, counts were completed in 1 day. Counts were usually made between 0700 and 1700 h.

Only pair data from counts made nearest 1 May and 1 June were used in the final breeding pair estimates and pairs per wetland analyses. Pair estimates for mallards, northern pintails, northern shovelers, and canvasbacks were based on early May counts, whereas estimates for gadwalls, blue-winged teal, redheads, lesser scaup, ring-necked ducks, and ruddy ducks were based on June counts. We used the higher of May or June counts for estimates of the pairs of American wigeon and green-winged teal.

Before 1967, nest searching methods included flailing the vegetation with switches or laths while walking through the cover in zigzag patterns, watching for hens to return to their nests, flushing hens from nests with dogs, towing ropes with tin cans, and finding nests during incidental field investigations. Because of the large variety and size of nesting habitats, those methods proved impractical. In late summer 1966 and early spring 1967, a cable–chain drag (Fig. 8) for finding duck nests was developed and tested (Higgins et al. 1969, 1971). The cable–chain drag has proven to be a practical method of finding a relatively large sample of duck nests in most types of upland prairie habitats; most nests in this study were found with this device.

Nest searches usually began the first week in May and were completed by mid-July each year. Three to four searches were made on the study

Fig. 8. Searching for upland duck nests with a cable-chain device on the Woodworth Study Area.

plots annually. Most were conducted between 0700 and 1600 h.

A nest was defined as a hollowed scrape containing one or more eggs. Nest locations were usually marked with a fluorescent red surveyor's flag trimmed to 3 cm wide, but in fields with tall, dense vegetation, nests were often marked with colored ribbon or cloth flags on willow sticks.

Nest markers were usually placed 3 m north of each nest. Standardization of marker direction from nests and flag color reduced the amount of time spent searching for nests during subsequent visits. A simple field map showing the general location and distance of a nest from obvious topographic features also reduced time spent finding these nests during revisits.

Data for each nest were recorded, in the field, on a standardized card (Fig. 9). Data recorded during the initial visit included date, time, location, number of eggs, stage of incubation, percent of dead vegetation at nest site, dominant plant species at the nest site, nest site physiognomy, overhead and side concealment of the nest, height of vegetation surrounding the nest, upland cover quality at and immediately surrounding the nest, and land use surrounding the nest.

The stage of embryo development of eggs in each nest was determined by candling in the field with a piece of flexible, 38 mm (1.5 inch) inside diameter black radiator hose (Weller 1956; Fig. 10), or by egg flotation in water (Westerskov 1950); the former method was preferred. Number of incubation days

Fig. 9. Data on duck species, nest site characteristics, land use, and clutch fate were recorded for each nest and map plotted at Woodworth Study Area.

plus number of eggs in a clutch were then used to calculate the date of nest initiation. Mean values for species' clutch sizes, incubation terms, and ages of clutches at hatching follow Klett et al. (1986).

Data recorded during subsequent nest visits included fate of clutch (destroyed, abandoned, or unknown), number of eggs hatched, amount of down, and cause of destruction if known. A successful nest was defined as one in which at least one duckling hatched and left the nest. Rates of nest success were estimated according to the Mayfield 40% method (Miller and Johnson 1978; Johnson 1979). Duck nest densities were calculated based on the number of nests per area searched. The sample of nests in all instances was those that survived long enough to be found because nearly all nests were found by flushing hens from their nests.

Brood counts were made annually to provide an index to production of ducklings in the study area. Every pothole with water was inventoried for broods or for hens doing distraction displays, which were considered as representing broods. Brood counts were made while wading through each wetland in undulating or zigzag patterns (Evans and Black 1956) to purposely flush hens and broods into an observation field for counting. The number and age class of ducklings were recorded according to Gollop and Marshall (1954). Records of broods by species, age, number of ducklings, and location were used to screen and separate duplicate records of broods counted earlier from ones counted later.

Two brood counts were made each year. The first was in early July when some ducklings on the area were known to be Age Class II-A or II-B, and

Fig. 10. Stage of egg-laying or incubation was determined for each clutch by candling, Woodworth Study Area.

one in early August. In 1965 and 1967 three brood counts were made. Incidental brood sightings also were recorded each summer. The annual total of broods for all species was the sum of flightless broods plus distraction–displaying hens minus duplicate observations among surveys. Occasionally, incidental brood observations were added to the total when a brood was known to have hatched after the last survey, as was the case in several years for ruddy ducks.

Only data from the regular brood counts were used in analyses of brood count and wetland data. Incidental brood observations were not used in these analyses and no adjustment was necessary for duplicate observations because of the time span between counts. An index of the annual rate of brood production (hen success) was calculated by dividing the estimated number of broods by the estimated number of pairs for each species.

Data Treatment

In 1952, the U.S. Fish and Wildlife Service (Service) established two areas of intensive waterfowl surveys and ecological research in prairie Canada (Smith 1971; Stoudt 1971). The study objectives emphasized the ecological factors that affect waterfowl production in the Canadian parkland areas of Alberta and Saskatchewan. In 1964, the Northern Prairie Wildlife Research Center, includ-

ing the Woodworth Field Station, was established in south-central North Dakota for the purpose of conducting waterfowl and wetland research.

An early task of the Center was to initiate studies similar to those being done by the Service in Canada. Work was begun to collect a set of long-term baseline data on the ecological and agricultural factors that affect waterfowl production in the United States portion of the prairie pothole region of the northern Great Plains. Much of the data collected during the Woodworth Station studies were from surveys and inventories and, for the most part, without a rigid design to facilitate statistical analyses. As such, most of the data treatment in this paper is more descriptive than statistical in nature. However, we have applied statistical treatment to some data sets to aid reader interpretation.

Because results of the two Canadian studies, as well as several other former studies, were presented in English equivalents only, we have either used metric and English together or have constructed our metric categories to match the size classes or unit increments (e.g., 40.5 ha equals 100 acres) of the former studies to aid direct comparisons.

The four authors have been associated with or knowledgeable about the overall studies on the Woodworth Station during the 17 years even though one transferred (HWM-1975) and one retired (LMK-1979) before the end of the data collection in 1981. We believe this continuity of involvement enhanced our ability to interpret and discuss the data and field observations.

We trust this report will be of importance to the overall international effort to better understand and manage the world's waterfowl populations.

Results and Discussion

Climate and Waterfowl Habitats

Daily, seasonal, and annual precipitation amounts fluctuated greatly on the WSA. These differences and their temporal distribution also affected wetland habitats, upland-nesting habitats, and trends in waterfowl populations occupying these habitats.

Bellrose (1979) reported that the abundance of ponds in the prairie pothole region is the most important single factor regulating the production of mallards and, no doubt, some other duck species. During 1965–81, percents of the 548 wetland basins that contained water were usually highest in early spring and lowest in late summer (Table 3). The wettest spring was in 1966 when 87% of the basins contained water, and the driest was in 1977 when only 8% of the basins had water. The mean percent of basins with water was 56% during 1–15 May surveys for the 17-year period.

Class III (seasonal) wetlands were the most numerous during 1965–75 (Table 4). Class IV (semipermanent) wetlands were less common than Class III wetlands but maintained more surface water and held water more consistently.

During 1965–75, an average of 50% or more of the wetlands with water were 0.2 ha or less, however, an average of 60% or more of the surface water area in wetlands was contained in 6–8% of the wetland basins and these were 4 ha or larger (Table 5).

Some wetlands with similar watersheds, basin morphology, vegetation, and watershed land use contained water while others did not during the

Table 3. *Percent of 548 basins containing water, Woodworth study area, 1965–81.*

Year	1–15 May	1–15 June	16–30 June	1–15 July	1–15 August
1965	71	63	52	48	60
1966	87	64	79	70	45
1967	81	66	60	38	22
1968	52	66	64	31	16
1969	69	61	57	54	50
1970	61	52	74	25	14
1971	34	49	41	33	7
1972	70	59	41	23	14
1973	29	10	5	3	2
1974	67	69	50	30	6
1975	79	71	71	72	44
1976	56	39[a]	—	19	8
1977	8	7	—	3	2
1978	61	—	—	26	4
1979	72	—	—	58	45
1980	25	—	17	12	5
1981	24	16	—	12	—

[a] — Indicates no survey.

Table 4. *Wetland class: average number and area during four survey periods, Woodworth Study Area, 1965–75.*

Wetland class	Mid-May		Early June		Early July		Early August	
	n	ha	*n*	ha	*n*	ha	*n*	ha
I — ephemeral	12	1	7	1	3	1	1	<1
I[t] — ephemeral tillage	2	1	1	1	1	1	0	0
II — temporary	43	8	31	6	15	3	6	2
II[t] — temporary tillage	2	1	1	<1	<1	1	<1	<1
III — seasonal	229	170	213	163	139	135	92	111
III[t] — seasonal tillage	4	3	3	4	2	4	1	3
T-2 — standing stubble	1	1	1	1	<1	1	0	0
T-3 — mulched stubble	<1	<1	0	0	<1	1	0	0
T-4 — summer fallow	2	1	1	1	<1	<1	<1	<1
IV — semipermanent	43	250	43	248	40	245	34	230
V — permanent	1	53	1	53	1	53	1	53
Dugout	1	1	1	1	1	1	1	1
Dam or stock dam	7	45	7	45	7	49	6	44
Total	347	535	310	524	209	495	142	444

[t] Superscript t indicates tillage.

Table 5. *Wetland size: average number and area during four survey periods, Woodworth Study Area, 1965–75.*

Size (ha)	Mid-May		Early June		Early July		Early August	
	n	ha	*n*	ha	*n*	ha	*n*	ha
≤0.09	56	3	41	2	23	1	11	1
0.10–0.25	91	16	79	14	45	7	26	5
0.26–0.50	77	28	72	27	45	15	28	11
0.51–0.75	30	18	29	17	22	12	15	9
0.76–1.00	23	20	22	19	16	13	11	9
1.01–2.00	33	45	31	43	23	37	21	30
2.01–5.00	21	64	20	62	19	55	16	48
5.01–10.00	3	20	3	19	3	17	2	16
10.01–25.00	9	148	9	147	9	147	8	136
≥25.01	4	168	4	168	4	168	4	168
Total	347	530	310	518	209	472	142	433

same years. Likewise, individual wetlands that were dry or nearly dry during wet years, were wet during dry years. Possibly these phenomena occur because of differences in groundwater flows. According to area soils maps, between 5 and 10% of the basins were situated on porous or gravelly soil substrates. These basins were not of substantial value to ducks because nearly all the runoff water went directly into groundwater storage or flowage.

At the WSA, we categorized years as wet for ducks when at least 65–75% of basins were full or nearly full of water during 1–15 May. Factors affecting the percent of wetland basins with water during the 1–15 May and 1–15 August counts were soil moisture conditions during fall freeze, amount of snow accumulation over winter, amount of snow during March, April, and sometimes May, speed of thawing during spring, and amount of heavy rainfall during March and April. The number of basins holding water in the previous August also had some effect on number of ponds with water in spring. To predict when a potential wet year would occur,

several combinations of precipitation measure were projected relative to the percent of basins containing water during early May and early August surveys (Table 6). The percent of wetlands with water during the 1–15 May counts had higher correlation with conserved soil moisture (Williams and Robertson 1965) for the 21-month period preceding 1 May ($r = 0.77$, $P < 0.0003$, 17 df) than with annual precipitation (Pospahala et al. 1974) in the previous 12-month period of 1 June–31 May ($r = 0.50$, $P < 0.04$, 17 df). There were no significant relations between precipitation amounts during the snow year, 1 September–1 May, or the crop year, 1 August–31 July ($P > 0.10$), and wet ponds during the 1–15 May counts.

The percent of wetlands with water during the 1–15 August counts (Table 6) was related to conserved soil moisture ($r = 0.74$, $P < 0.0008$, 17 df). There were no significant relations between the 1–15 August counts of wetlands with water and precipitation during the snow year, the calendar year, or in the 12-month period (crop year) preceding 1 August ($P > 0.10$). An explanation for the weakness of relations with some of the precipitation variables may be the lack of data for a series of consecutive wet or dry years. During this study, wet and dry years were usually single-year events.

In this region, upland habitats provided nearly all the nesting cover for dabbling duck species and lesser scaup whereas most other diving ducks nested overwater in emergent cover. However, some overwater nesting by dabbling ducks did occur in and near the area (Krapu et al. 1979). Although we did not measure the structural characteristics of the upland habitats, there were obvious differences in height and quantity of cover each year; probably related to precipitation and soil moisture conditions. In general, good-to-excellent nesting cover was available in years with average or above average precipitation and fair-to-poor in below average precipitation years. As with wetland water conditions, upland cover structure varied

Table 6. *A comparison of three measurement methods of precipitation or snowfall to early spring and late summer wetland conditions, Woodworth Study Area.*

Year	Past winter's snowfall 1 September – 31 May (inches)	Calendar year precipitation (inches)	Crop[a] year precipitation 1 August– 31 July (inches)	Percent of 548 basins containing water 1–15 May	Percent of 548 basins containing water 1–15 August
1964	15[b]	21.44	20.56	no data	no data
1965	31.5	22.92	16.52	71	60
1966	42[c]	13.82	22.18	87	45
1967	37	9.22	8.57	81	22
1968	21.5	17.53	16.38	52	16
1969	56	12.89	16.12	69	50
1970	39.5	13.26	12.39	61	14
1971	31	17.62	14.94	34	7
1972	26.5	12.43	14.20	70	14
1973	17.5	16.41	10.89	29	2
1974	23.5	14.89	20.43	67	6
1975	37.5	19.90	19.15	79	44
1976	36.5	8.37	12.36	56	8
1977	25	21.40	12.99	8	2
1978	22.5	14.21	19.58	61	4
1979	57.5	15.57	16.50	72	45
1980	23	17.69	11.35	25	5
1981	18	15.12	16.56	24	12[d]
Mean (n = 18)	31.0	15.82	15.65	56	21

[a] From 1 August of preceding year to 31 July of calendar year.
[b] April snow amounts were missing but 2.59 inches of moisture was measured. Arrowwood NWR showed 7.8 cm of snow for April.
[c] 24 inches was measured from March blizzard.
[d] Late July survey.

greatly among months and seasons but was usually better when soil moisture was continuously high during sequences of wet falls and springs. Frequent, small rains were believed better than a large, single rain for nesting cover growth.

Breeding Pairs

Chronology of Arrivals

The dates migrating waterfowl arrived in spring at the WSA were highly variable among years, probably because spring weather over northern latitude prairies is uncertain. The earliest arrival was 15 March for mallards and northern pintails, whereas the latest was 16 May for ruddy ducks (Appendix E). During most springs, the first sighting of a species was usually followed by an influx of pairs within a few days to a week. Mallards and northern pintails were usually followed by redheads, American wigeon, gadwalls, lesser scaup, and ring-necked ducks between 25 March and 10 April; canvasbacks, green-winged teal, northern shovelers, and blue-winged teal between 1 and 20 April; and ruddy ducks between 20 April and 15 May.

Hammond and Johnson (1984), reporting on mallards, gadwalls, blue-winged teal, and redheads, found that arrival dates varied with mean temperatures before and during the usual arrival period for each species. Warm spring weather induced earlier arrival and nesting on the WSA. Arrival dates were most affected by temperature for mallards during 12–25 March, for redheads 12 March–8 April, for gadwalls 26 March–8 April, and for blue-winged teal 26 March–15 April. Warm spring weather also seemed to induce earlier nesting; mallards were affected most by temperature during April and the others by temperature during late April and May.

Pair Count Periods and Species Composition

We made the first pair counts during the first 2 weeks in May and a second count during the last week of May or the first 2 weeks in June. The first count closely coincided with the first blue-winged teal nest initiations and the second with the first gadwall nest initiations. Our census periods approximated those of Dzubin (1969), Smith (1971), and Stoudt (1971).

The mean composition of breeding pairs during 1965–81 was 86% dabblers (range 73–97%) and 14% divers (range 3–27%) (Table 7). These means compare favorably with Evans and Black (1956) for South Dakota, Dzubin (1969) for Manitoba, Henry et al. (1972) from May aerial surveys for the Prairie Provinces and Dakotas, Kiel et al. (1972) for Manitoba, and Trauger and Stoudt's (1978) study areas, one in Alberta and one in Saskatchewan. Dzubin (1969) had more dabbling ducks (97%) in the populations at Kindersley, Saskatchewan, and Trauger and Stoudt (1978) had a smaller percent of dabbling ducks (70%) in their Manitoba study areas.

Major fluctuations in species composition occurred over time; however, percent compositional changes were less pronounced than estimates of pair numbers because all species did not change proportionately within years. Percent composition of dabbling ducks was higher than average for all years 1965–73, whereas, beginning in 1974, dabbling duck percent composition was average or below average for all years 1974–81 (except 1976).

Blue-winged teal were the most abundant species, making up an average of 46% of the pair estimate. The next most abundant (between 10 and 15%) were gadwalls and mallards. All other species (Table 7) average less than 10% abundance; ring-necked ducks were scarcest (<1%). The average species composition at the WSA (Table 7) was nearly the same as that reported by Evans and Black (1956) during 1950–53 at Waubay, South Dakota. More lesser scaup at the WSA was the only minor exception between the two areas. This suggests that the species composition of ducks in the Dakotas has remained rather similar during the past 30–35 years.

Number of Pairs and Wetland Occupancy

Total pairs of ducks on the area averaged 492 and varied from 236 to 692 during 1965 through 1981 (Table 8). The density of duck pairs averaged $40/km^2$ during the 17 years and ranged from 19 to $56/km^2$. The density of basins with surface water during 1–15 May for the same period averaged $25/km^2$ and ranged from 3 to $39/km^2$.

The average number of pairs per 2.6 km^2, by species, was: blue-winged teal, 47; gadwalls, 14; mallards, 11; northern pintails, 7; northern shovelers, 6; lesser scaup, 5; redheads, 4; ruddy ducks, 4;

Table 7. *Percent species composition of pairs of ducks, Woodworth Study Area, 1965–81.*

Species	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	Min–Max	$\bar{x}$
Dabbling ducks																			
Mallard	8	10	8	14	8	11	12	14	18	7	9	12	15	11	7	13	12	7–18	11
Gadwall	14	17	11	14	11	16	17	15	19	12	12	14	17	14	9	14	15	9–19	14
Northern pintail	8	6	6	3	6	8	8	6	7	8	6	4	6	7	4	10	4	3–10	6
Green-winged teal	2	2	2	2	3	2	4	3	4	1	1	1	2	1	<1	2	2	1–4	2
Blue-winged teal	41	46	63	52	49	43	41	45	32	47	45	54	35	49	51	31	31	31–63	46
Northern shoveler	8	4	5	6	7	6	5	5	5	3	5	5	6	8	10	8	5	3–10	6
American wigeon	3	2	2	2	2	3	3	4	5	2	1	1	3	2	1	3	2	1–5	2
Total dabbling ducks	84	87	97	92	85	90	90	91	91	80	80	90	84	84	83	81	73	73–97	86
Diving ducks																			
Redhead	3	4	1	3	3	2	2	1	1	5	5	5	1	6	6	5	4	1–6	4
Canvasback	3	1	0	<1	<1	1	<1	<1	1	<1	1	1	2	<1	2	4	4	0–4	1
Lesser scaup	3	5	1	3	6	7	6	6	7	6	5	3	9	3	4	7	8	1–9	5
Ruddy duck	6	2	1	2	5	<1	<1	1	1	9	9	1	3	6	5	3	12	<1–12	4
Ring-necked duck	0	1	<1	0	<1	<1	1	0	1	0	<1	<1	1	<1	<1	<1	0	0–1	<1
Total diving ducks	15	13	3	8	15	10	10	9	9	20	20	10	16	16	17	19	27	3–27	14
Total pairs	638	519	574	477	466	547	286	485	318	499	692	643	236	575	609	472	329	236–692	492

Table 8. *Number of pairs of ducks, Woodworth Study Area, 1965–81.*

Species	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	Min–Max	$\bar{x}$
Dabbling ducks																			
Mallard	51	52	47	68	37	62	35	66	57	33	65	78	35	61	45	63	40	33–78	53
Gadwall	92	86	60	67	53	86	48	74	61	61	83	92	41	79	53	66	50	41–92	68
Northern pintail	53	32	33	14	28	46	24	28	23	38	43	26	15	41	25	49	13	13–53	31
Green-winged teal	15	10	13	7	12	12	11	12	14	4	6	5	4	8	2	10	8	2–15	9
Blue-winged teal	261	236	363	248	227	237	117	216	103	234	314	345	83	283	311	144	103	83–363	225
Northern shoveler	53	23	29	26	31	35	15	26	15	16	34	29	14	46	62	36	17	14–62	29
American wigeon	16	12	14	9	9	15	8	17	16	11	7	6	6	12	6	13	8	6–17	11
Total dabbling ducks	541	451	559	439	397	493	258	439	289	397	552	581	198	485	504	381	239	198–581	424
Diving ducks																			
Redhead	16	18	5	14	16	9	6	7	2	25	35	34	2	35	38	25	13	2–38	18
Canvasback	22	6	0	2	2	6	1	1	2	2	9	3	4	3	14	18	14	0–22	6
Lesser scaup	19	28	4	13	28	36	17	30	21	32	34	16	22	16	23	31	25	4–36	23
Ruddy duck	40	11	4	9	22	1	1	8	2	43	61	8	7	35	29	15	38	1–61	20
Ring-necked duck	0	5	2	0	1	2	3	0	2	0	1	2	3	1	1	2	0	0–5	1
Total diving ducks	97	68	15	38	69	54	28	46	29	102	140	62	38	90	105	91	90	15–140	68
Total pairs	638	519	574	477	466	547	286	485	318	499	692	643	236	575	609	472	329	236–692	492

American wigeon, 2; green-winged teal, 2; canvasbacks, 1; and ring-necked ducks, <1. The greatest pair densities per 2.6 km^2, by species, was: blue-winged teal, 76; gadwalls, 19; mallards, 16; northern shovelers and ruddy ducks, 13; northern pintails, 11; lesser scaup and redheads, 8; canvasbacks, 5; American wigeon, 4; green-winged teal, 3; and ring-necked ducks, 1. The greatest total density of pairs was 56/km^2 in 1975. This density was about half the pair density of 116/km^2 Smith (1971) counted at Lousana, Alberta, in 1958.

The percent of wetlands containing one or more pairs of ducks in mid-May counts during 1965–75 varied from 24.3 to 44.8% and averaged 36.8% (Table 9); late May and early June counts varied from 33.7 to 85.5% and averaged 47.5% (Table 10). The number of wetlands with pairs was directly related to shoreline length (Table 11) and to size class (Table 12) of wetlands. These relations were consistent for all duck species; that is, large wetlands were more likely to have pairs than small ones.

The 11-year mean of 36.8% occupancy of wetlands by duck pairs in mid-May at the WSA was lower than the 14-year mean of 46.0% in Saskatchewan (Stoudt 1971) and the 13-year mean of 55.0% in Alberta (Smith 1971), but the 47.5% average occupancy rates for late May and early June counts compare favorably to those of Smith (1971) and Stoudt (1971).

The WSA data, like those of Smith (1971) and Stoudt (1971), suggested that the percent of pair occupancy of wetlands varied inversely with the number of wet basins; that is, the number of wet basins declined through the summer and the percent occupancy of the remaining wet basins increased until approximately the end of the nesting period (late June–early July). Percent pond occupancy by ducks can vary on small study areas or even on individual wetlands due to time of day (Diem and Lu 1960; Dzubin 1969; Klett and Kirsch 1976), or night (Drewien et al. 1967), observability (Sauder et al. 1971), and social behavior among species such as spatial demands (Bellrose 1979). Pond occupancy rates could seem similar over time if quantities of ponds and ducks were declining at the same time, a condition that is probably happening in the prairie pothole region today.

Smith (1971) contended that low habitat (wetlands) occupancy means little unless the circumstances surrounding it are also understood. He further stated that it may reflect an absence of potholes or an absence of ducks. Smith (1971) found that even when duck numbers were large (116 pairs per square kilometer), only 72% of the wetlands were occupied by ducks during one time.

Some recent studies have revealed that the number of wetlands (Bellrose 1979) or amount of water (Kaminski and Prince 1984) affect duck abundance, and that duck distribution varies among wetlands in relation to temporal and spatial distribution of food items (Swanson 1977; Swanson et al. 1974; Swanson et al. 1979). Thus, locally, individual pond occupancy by ducks is dependent on the total duck density and wetland conditions within a complex of different classes of wetlands varying over time. On a larger scale, pond occupancy rates in one State, Province, or region may be greater or smaller during the same season or year because of differences in water conditions in another part of the country. This may cause ducks to stop further south during wet times and overfly to the north during dry times (Smith 1970; Pospahala et al. 1974).

Findings from our study show that pond occupancy data collected by periodic surveys during several years are, at best, weak indexes of specific selection behavior of ducks to various wetland characteristics. However, we believe the data show some meaningful trends and insights into wetland habitat preference by ducks. We caution against using pond occupancy data from a single study area, such as ours, to project possible national trends in continental waterfowl populations. If pond occupancy rates are to be meaningful on a continental basis, we recommend a large coordinated effort over time and area to support the considerable concern about our declining waterfowl numbers today.

Pair Relations to Wetland Size

An inverse relation was apparent between total estimated duck densities and wetland size (Table 13; Figs. 11 and 12), indicating greater densities of ducks could be expected on wet ponds of smaller size classes. Larger and deeper wetlands were utilized more by dabbling duck pairs in dry years than in wet years. Dabbling ducks utilized seasonal wetlands more than other wetland classes; however, they also used semipermanent

Table 9. *Mean percent occupancy of wet ponds by duck pairs of all species on mid-May counts, Woodworth Study Area, 1965–75.*

	Percent occupancy of wetlands with water											
Species — Year / *n* ponds	1965 393	1966 425	1967 411	1968 370	1969 351	1970 338	1971 195	1972 384	1973 156	1974 371	1975 412	$\bar{x}$ 346
Dabbling ducks												
Mallard	8.9	9.4	8.0	12.1	6.6	9.2	18.5	11.7	19.9	8.1	5.8	9.8
Gadwall	8.9	11.5	12.2	10.3	12.3	11.2	19.0	8.1	14.7	7.0	9.2	10.7
American wigeon	2.0	2.1	1.9	2.2	2.6	4.1	5.6	2.9	5.1	2.4	1.5	2.7
Green-winged teal	1.3	2.6	2.7	3.2	1.1	4.4	3.6	1.3	7.1	1.9	1.0	2.4
Blue-winged teal	26.7	26.8	35.8	27.8	34.5	27.8	29.7	19.0	14.1	16.2	26.7	26.5
Northern shoveler	9.7	4.9	2.9	4.3	4.6	8.9	6.7	5.7	5.1	1.6	5.6	5.4
Northern pintail	6.6	4.9	5.6	2.4	5.7	5.6	7.2	8.1	9.0	4.6	5.1	5.6
Total dabbling ducks	35.6	37.2	43.6	37.6	41.0	37.3	41.5	34.9	31.4	24.0	34.5	36.3
Diving ducks												
Redhead	2.0	1.9	1.7	2.2	2.3	3.0	1.0	0.5	1.3	2.7	3.2	2.0
Canvasback	1.0	0.0	0.2	1.1	0.0	0.0	0.5	0.3	0.0	0.3	1.0	0.4
Lesser scaup	1.8	2.8	4.9	2.4	2.3	2.7	3.1	2.6	2.6	1.9	1.7	2.6
Ring-necked duck	0.3	0.5	0.5	0.0	0.9	2.1	1.5	0.5	1.3	0.5	1.0	0.7
Ruddy duck	1.0	1.2	0.7	0.3	1.1	1.2	1.0	0.5	0.0	0.3	1.0	0.8
Total diving ducks	3.8	4.0	6.3	4.9	4.6	5.0	4.6	2.9	3.8	4.3	4.4	4.4
Total pairs	36.4	37.4	44.8	38.1	41.0	37.3	42.1	35.2	32.1	24.3	35.2	36.8

Table 10. *Mean percent occupancy of wet ponds by duck pairs during late May–early June counts, Woodworth Study Area, 1965–75.*

Species		Mean percent occupancy of wet ponds										
	Year	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	$\bar{x}$
	n	344	352	363	362	336	286	267	320	55	368	359	310
Dabbling ducks												
Mallard	8.7	11.4	11.0	12.4	6.5	12.9	9.0	12.5	52.7	6.3	11.4	10.9
Gadwall	17.7	18.8	12.9	13.2	12.2	17.8	13.9	14.7	63.6	12.8	19.2	16.1
American wigeon	3.2	2.3	2.8	2.2	2.1	4.5	3.0	4.1	18.2	2.2	1.7	3.0
Green-winged teal	3.5	2.6	3.0	2.5	3.0	3.8	4.1	2.5	5.5	1.1	1.1	2.7
Blue-winged teal	41.3	40.3	48.8	30.7	39.6	36.0	24.7	34.1	67.3	35.9	47.4	38.7
Northern shoveler	10.8	6.0	7.4	4.4	7.4	10.5	4.9	6.6	18.2	3.5	7.8	7.1
Northern pintail	11.6	7.7	6.9	2.5	5.4	9.4	7.5	5.3	18.2	7.6	7.8	7.3
Total dabbling ducks	50.9	49.7	56.7	38.7	46.1	43.7	33.3	42.5	85.5	44.8	53.8	47.1
Diving ducks												
Redhead	2.3	2.6	0.6	1.7	2.4	2.4	1.9	0.9	3.6	2.2	5.0	2.2
Canvasback	0.9	1.1	0.0	0.0	0.3	0.0	0.4	0.0	1.8	0.0	0.3	0.3
Lesser scaup	2.6	1.1	0.8	1.1	2.7	3.1	2.6	3.4	14.5	2.2	1.7	2.3
Ring-necked duck	0.0	0.6	0.6	0.0	0.6	0.0	0.7	0.0	1.8	0.0	0.0	0.3
Ruddy duck	1.7	1.4	0.3	0.3	1.2	0.0	0.4	0.6	3.6	2.4	3.6	1.3
Total diving ducks	4.9	5.4	1.9	2.8	4.8	5.2	4.9	3.4	16.4	5.2	6.7	4.7
Total pairs	51.2	50.9	57.0	39.0	46.4	44.1	33.7	42.5	85.5	45.7	54.3	47.5

Table 11. *Mean percent occupancy by duck pairs in wet ponds by perimeter length during late May–early June counts, Woodworth Study Area, 1965–75.*

Species	Mean percent occupancy of wet ponds with perimeter length (m)							
Perimeter length	≤100	100–249	250–499	500–749	750–999	1,000–1,999	2,000–5,000	≥5,000
Average no. ponds per year	8	43	97	71	30	43	15	3
Dabbling ducks								
Mallard	2.2	1.5	4.0	9.3	13.8	21.4	48.5	60.6
Gadwall	0.0	2.8	6.9	14.9	21.6	29.1	67.1	78.8
American wigeon	0.0	0.6	0.9	1.5	3.6	4.9	18.0	36.4
Green-winged teal	0.0	0.4	1.4	2.1	3.3	4.7	11.4	21.2
Blue-winged teal	18.7	13.6	27.7	37.8	52.7	63.0	88.6	93.9
Northern shoveler	2.2	0.9	3.1	4.4	9.0	14.5	34.1	39.4
Northern pintail	2.2	0.9	3.3	6.3	10.2	15.6	23.4	39.4
Total dabbling ducks	22.0	17.9	35.3	47.8	65.0	73.5	95.2	97.0

Diving ducks								
Redhead	0.0	0.0	0.1	1.0	2.4	3.0	18.0	45.5
Canvasback	0.0	0.0	0.0	0.1	0.0	0.6	1.8	12.1
Lesser scaup	0.0	0.2	0.3	0.5	1.8	2.8	20.4	51.5
Ring-necked duck	0.0	0.0	0.1	0.1	0.0	0.2	0.0	18.2
Ruddy duck	0.0	0.0	0.0	0.1	0.6	0.6	18.0	24.2
Total diving ducks	0.0	0.2	0.5	1.5	4.5	6.6	40.7	84.8
Total pairs	22.0	18.1	35.4	48.3	65.3	74.6	96.4	100.0

Table 12. *Mean percent occupancy by duck pairs in wet ponds by size class late May–early June counts, Woodworth Study Area, 1965–75.*

	Mean percent occupancy of wet ponds in size class (ha)									
Size class	≤0.09	0.1–0.25	0.26–0.5	0.51–0.75	0.76–1.0	1.01–2.0	2.01–5.0	5.01–10.0	10.01–25.0	≥25.01
Species Average number per year	41	79	72	29	22	31	20	3	9	4
Dabbling ducks										
Mallard	2.2	3.3	6.0	12.4	15.6	15.8	29.6	35.3	55.1	50.0
Gadwall	0.9	6.7	10.3	17.5	20.2	22.3	44.4	58.1	76.5	75.0
American wigeon	0.0	0.9	1.3	2.2	4.9	3.2	6.7	9.7	29.6	15.9
Green-winged teal	0.4	1.3	1.9	2.5	4.1	3.2	4.0	3.2	16.3	20.5
Blue-winged teal	12.7	27.3	30.1	43.9	52.3	59.8	74.9	77.4	89.8	90.9
Northern shoveler	0.9	2.8	3.5	5.4	8.2	11.1	21.5	22.6	43.9	27.3
Northern pintail	1.5	2.3	5.0	7.0	10.3	12.9	17.9	22.6	33.7	25.0
Total dabbling ducks	16.5	33.9	39.6	53.2	64.6	17.6	84.8	96.8	95.9	93.2
Diving ducks										
Redhead	0.0	0.0	0.3	1.6	2.1	3.5	4.9	9.7	29.6	20.5
Canvasback	0.0	0.0	0.0	0.3	0.4	0.3	0.4	3.2	5.1	2.3
Lesser scaup	0.2	0.3	0.1	1.3	0.4	2.6	4.0	3.2	30.6	43.2
Ring-necked duck	0.0	0.1	0.0	0.3	0.0	0.0	0.4	0.0	4.1	4.5
Ruddy duck	0.0	0.0	0.0	0.3	0.0	0.6	1.8	9.7	23.5	25.0
Total diving ducks	0.2	0.5	0.4	2.9	2.5	6.7	10.8	22.6	55.1	65.9
Total pairs	16.7	33.9	39.9	53.8	65.0	73.0	85.2	100.0	96.9	95.5

Table 13. *Regression coefficients for duck pairs from wetland size, Woodworth Study Area, 1965–75.*

Species and wetland class	Regression coefficients $\sqrt{area}$ b_1	$\sqrt{area}$ b_2	Overall significance level
Mallard			
Temporary	0.22*	−0.05	0.0001
Seasonal	0.04*	0.10*	0.0001
Semipermanent	−0.01	0.23*	0.0001
Gadwall			
Temporary	0.05	0.04	0.08
Seasonal	0.10*	0.08*	0.0001
Semipermanent	0.06	0.18	0.0001
Northern pintail			
Temporary	0.35*	−0.06	0.0003
Seasonal	0.06*	0.03*	0.0001
Semipermanent	−0.00	0.10*	0.0001
Green-winged teal			
Temporary	0.18*	−0.06*	0.0001
Seasonal	0.02*	0.00	0.0001
Semipermanent	−0.01*	0.05*	0.0001
Blue-winged teal			
Temporary	0.42	0.10	0.0001
Seasonal	0.20*	0.53*	0.0001
Semipermanent	−0.13*	1.29*	0.0001
American wigeon			
Temporary	0.01	0.01	0.18
Seasonal	0.01*	0.02*	0.0001
Semipermanent	−0.01*	0.05*	0.0004
Redhead			
Temporary	0.00	0.00	—[a]
Seasonal	0.03*	−0.02*	0.0001
Semipermanent	−0.00	0.16*	0.0001
Canvasback			
Temporary	0.00	0.00	—
Seasonal	0.003*	−0.00	0.0001
Semipermanent	0.01	0.05	0.0017
Lesser scaup			
Temporary	0.05*	−0.01	0.0039
Seasonal	0.06*	−0.06*	0.0001
Semipermanent	0.02*	0.01	0.0001
Ruddy duck			
Temporary	0.00	0.00	—
Seasonal	0.05*	−0.04*	0.0001
Semipermanent	0.08*	−0.06	0.0001
Dabbling ducks			
Temporary	1.32*	−0.03	0.0001
Seasonal	0.44*	0.80*	0.0001
Semipermanent	−0.06	1.87*	0.0001

Table 13. *Continued.*

Species and wetland class	Regression coefficients $\sqrt{area}$ b_1	$\sqrt{area}$ b_2	Overall significance level
Diving ducks			
Temporary	0.05*	-0.01	0.0039
Seasonal	0.15*	-0.13*	0.0001
Semipermanent	0.11*	0.16	0.0001

[a] Indicates no data.
* Indicates significant coefficients at the $P < 0.05$ level.
Note: Pair counts are average values for 1965–75 and pairs = $b_1 \sqrt{area} + b_2 \sqrt{area}$ where area is in acres.

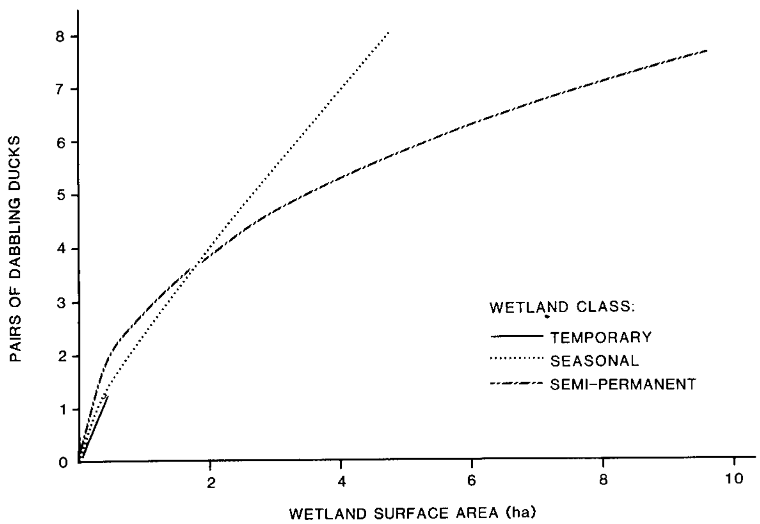

Fig. 11. Relation of dabbling duck pairs to size and class of wetlands, 1965–75.

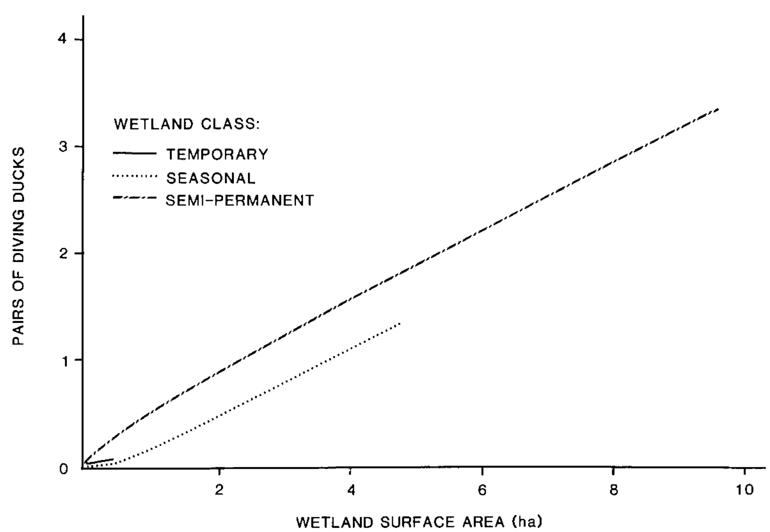

Fig. 12. Relation of diving duck pairs to size and class of wetlands, 1965–75.

wetlands frequently when those were less than 2 ha. With the exception of lesser scaup, diving ducks generally used semipermanent wetlands of all size classes in greater proportion than dabbling ducks; diving ducks generally accepted wet ponds of greater size, regardless of wetland classes. This was particularly true for ruddy ducks. Differences in feeding behavior offer a possible explanation of the contrasting relations of dabbling and diving duck pair densities to wetland size. Diving ducks utilize the total area of larger wetlands by diving for food, regardless of emergent vegetation cover or water depth, whereas dabbling ducks feed more in smaller and shallower wetlands and seldom use the central or open unvegetated areas of larger wetlands. By using this difference and calculating dabbling duck pair densities in relation to a peripheral band, for example, a 35 m width outward from the shore instead of the whole surface area of wetlands, larger than 6 ha, we suspect the comparison of pair density ratios would be more meaningful. If this concept is true, it has important implications for wetland preservation and management. Figure 13 illustrates opposite relations of pair densities to two different characteristics of wetlands (surface area vs. shoreline length) and this, we believe, suggests that the surface area of wetlands being utilized influences the spatial distribution of pairs more than the effects of the spatial density of pairs (or indicators of pairs such as lone males) to one another.

In summary, wetlands of all sizes and classes were used at some time by one species of duck or another. Smaller (<0.2 ha), temporary and seasonal wetlands were important early in the season for attracting, holding, and regulating the abundance of the duck population that would later nest on the area. Medium-sized and larger wetlands and wetlands of seasonal, semipermanent, and permanent classes provided water throughout the nesting and brood-rearing seasons. Seasonal wetlands were believed to be the most important overall. Species, with the exception of canvasbacks, redheads, and ruddy ducks, required a complex of various sizes and classes of wetlands throughout a production season because time-related activities of ducks, wetland plants and other animals had phenologically different distributions. Seldom does a single wetland provide all the essentials for breeding, nesting, and brood rearing at the right time or during a whole season. Programs for wetland protection, either by lease, easement, or fee title, must consider wetland complexes if all duck species in an area are to benefit. This, of course, affects the strategies of agencies involved in wetland preservation or waterfowl production, or both.

Pair-to-wetland Relations

There was a significant positive linear relation ($r^2 = 0.64$, $P < 0.001$, 16 df) between the total estimated duck pairs per year and the percent of basins with water during 1–15 May (Fig. 14). This relation was also examined for each species (Table 14). Total dabbling duck pairs were related ($r^2 = 0.81$) better with the early May percent of wet basins than diving duck pairs ($r^2 = 0.28$). Blue-

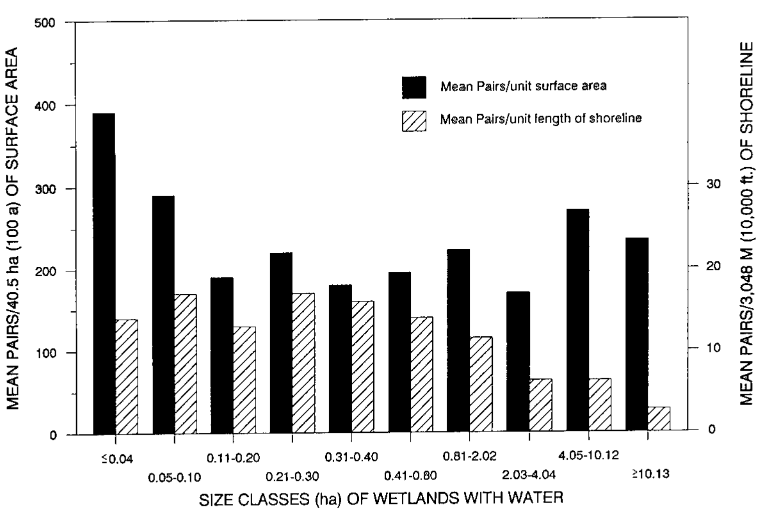

Fig. 13. Comparison of mean pair densities for all duck species between surface area and shoreline length of wetlands, Woodworth Study Area, 1965–75.

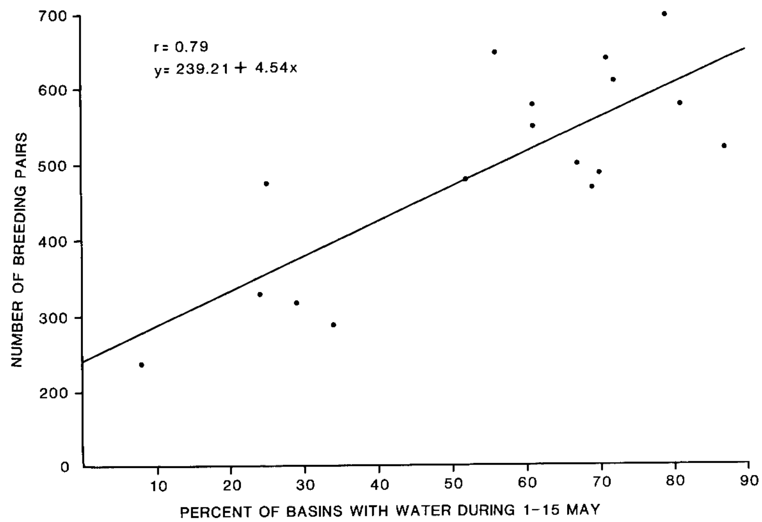

Fig. 14. Breeding duck pairs of all species in relation to percent of 548 basins with water during 1-15 May, Woodworth Study Area, 1965-81.

winged teal were the most responsive to percent of wet ponds. We think the lack of a stronger regression between estimated pairs and percent of basins with water is partially because basin fullness and basin water depth were not taken into account.

Schroeder (1971) and Stewart and Kantrud (1974) also found significant correlations between May surface water and duck pairs in North Dakota. Many studies have shown positive correlations between the number of wet pothole basins and duck pair populations; these studies are summarized by Dzubin (1969) and Stewart and Kantrud (1974).

Anderson and Glover (1967) found a strong relation between the number of duck pairs and early spring water at Monte Vista National Wildlife Refuge, Colorado. Boyd (1981) found a stronger relation between duck numbers and a soil moisture index than with the number of ponds estimated during aerial surveys. We agree with Boyd (1981), that for ducks, the effects of sequences of dry or wet years are greater than those of a single season. To have a series of wet years, an area would need to have consistently greater than normal precipitation and high spring runoff with an average or above average ratio of precipitation to evaporation. Winter and Carr (1980) recently demonstrated that persistence in basin water conditions is also strongly related to groundwater flows and closeness of the groundwater table to terrain surface, further complicating prediction of wet year wetland conditions.

More intensive studies are needed of the connection between duck populations and water conditions in the prairie pothole region. This area can be in a drought during 1 month or season and saturated with water the next. Long-term studies of temporal variables of precipitation and soil moisture indices, similar to that of Boyd (1981), seem appropriate and timely, especially for agencies involved in future intensive regulation of the annual sporting harvest of waterfowl in North America.

Table 14. *Correlation coefficients between duck pairs per year and 1-15 May water counts, Woodworth Study Area, 1965-81.*

Species	r-values[a]
Dabbling ducks	
Mallard	0.1908
Gadwall	0.5518
Northern pintail	0.4261
Green-winged teal	0.1013
Blue-winged teal	0.8267
Northern shoveler	0.4608
American wigeon	0.2140
Total dabbling ducks	0.8135
Diving ducks	
Redhead	0.3757
Canvasback	-0.0767
Lesser scaup	0.0407
Ruddy duck	0.2897
Ring-necked duck	-0.0883
Total diving ducks	0.2811
Total pairs	0.7966

[a] r-values >0.48 were significant, at 16 df.

Similar to Boyd's (1981) work with wetlands, Hanson et al. (1982) investigated the linear dependence between the current year's precipitation (1 August–31 July) and the previous 2 year's precipitation they found no dependence between forage yield and seasonal precipitation, suggesting that the dependence between yields must be associated with other factors such as soil water, plant vigor, and other biological factors. They did find an indication that during years of below-average yield there was a reduced probability of a good yield the next year. During the 51-year (1930–80) herbage yield study, Hanson et al. (1982) found only two occurrences of three consecutive below-average yields, both in the early 1960's, and four occurences of 3 sequential years of above-average yields, one group during the mid-1950's and the other during the late 1960's. These periods coincide with Boyd's (1981) lowest projected number of dabbling ducks in May 1962 and the highest number in May 1956. We point this out to demonstrate that two independent researchers, one working on wetland habitats (Boyd 1981) and the other on range forage yield (nesting cover; Hanson et al. 1982), had similar conclusions based on historical climatic records. The condition of the two habitats is probably related and most probably to soil mositure or precipitation, or to a precipitation–evaporation ratio, or a combination of these.

Waterfowl Nesting and Production

Ducks, eggs, and ducklings suffer an array of fatal factors on the breeding grounds. We believe the long-term nature of this study and the relatively large sample of nests and brood observations each year provide useful data on the relations of duck nesting, brood production, types of habitat use, and the influence of habitat on predation.

Upland-nesting Species

During the study, 3,832 duck nests were found in grassland and grass–shrubland habitats: 56% belonged to blue-winged teal, 18% were gadwalls, 11% mallards, 6% northern pintails, 5% northern shovelers, 2% American wigeon, 2% green-winged teal, and 1% lesser scaup (Table 15). Pair estimates and nests found were in similar proportion to species present except for blue-winged teal and lesser scaup. The percent of blue-winged teal nests was higher than the percent for pairs (56 vs. 46%) and the percent of lesser scaup nests was lower than the percent of pairs (1 vs. 5%). Because blue-winged teal have a relatively low reflushing rate (70%) with our nest searching device, but make up a large portion of the duck population, it seems probable that the discrepancy in proportions of percent composition by teal may be more related to counting and tabulation of blue-winged teal pairs than finding their nests. On the basis of some marked bird observations and years of counting experience, we propose the hypothesis that many lone drake blue-winged teal do not truly represent a pair but are in fact just bachelor drakes. With lesser scaup, we believe the relative discrepancy probably occurs in the pair estimates because not all lesser scaup seen in spring represent nesting pairs, specifically the yearling females (Trauger 1971, 1975).

Nesting Period

The nesting period for dabbling ducks from first egg laid (Fig. 15) until the last egg hatched was from 7 April to 12 August. There was little fluctuation in the nesting chronology from year to year. Overall, nest initiations inclusive of renests as well as initial nesting attempts, ranged from 7 April to 14 July. This range is probably conservative because it is based on backdating only active nests.

Spring migration and early nest initiations at the WSA were invariably interrupted by weather. An extreme example of this occurred in 1967 when nesting species (except ruddy ducks) arrived between 23 March and 12 April, an early and short arrival period. However, during 1–3 May 1967, a blizzard occurred; winds reached 97 kph, temperatures dropped to -9° C and 15 cm of snow fell. By the morning of 2 May, most of the smaller (<0.4 ha) potholes were frozen solid enough to support a man. The northward migration of waterfowl and some early nests were disrupted by this storm. The only ducks remaining in the area congregated on the unfrozen, larger potholes and lakes. The physiological effects to and deaths of waterfowl at Woodworth and in other parts of the storm area were reported by Bry (1967, 1970), and Dane and Pearson (1971).

Mallards, northern pintails, blue-winged teal, and northern shoveler were the earliest nesting

Table 15. *Number of duck nests by upland nesting species and year, Woodworth Study Area, 1966–81.*

Species	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	Total
Mallard	4	13	18	13	38	30	44	27	13	27	48	33	51	18	16	17	409
Gadwall	16	21	23	28	36	56	80	42	73	73	56	45	65	16	25	33	688
American wigeon	3	0	0	2	8	4	17	3	2	2	4	3	8	1	0	3	60
Green-winged teal	3	8	5	5	10	2	7	2	3	4	2	0	5	0	0	1	57
Blue-winged teal	34	96	98	92	176	128	180	101	212	325	216	62	236	69	39	67	2,131
Northern shoveler	0	9	8	16	14	10	24	3	15	19	17	7	29	13	2	10	196
Northern pintail	5	5	3	16	26	16	22	9	20	19	16	15	25	23	7	11	238
Lesser scaup	0	4	2	9	6	3	7	1	4	1	4	0	5	0	1	6	53
Total	65	156	157	181	314	249	381	188	342	470	363	165	424	140	90	147	3,832

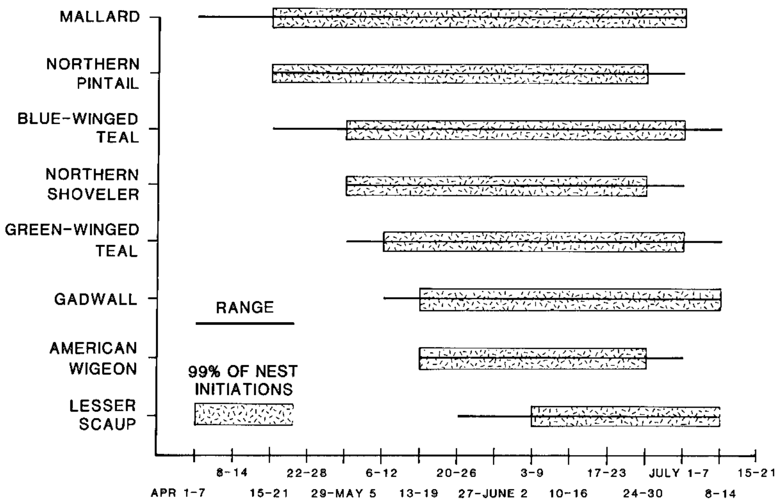

Fig. 15. Seasonal nest initiation chronology of upland nesting ducks, Woodworth Study Area, 1966–81.

species (Fig. 15). In fact, at our location, blue-winged teal and northern shovelers should probably be considered early-nesting species. Next in order were green-winged teal, gadwalls, American wigeon, and lesser scaup. Mallards, northern pintails, and blue-winged teal continued initiating nests over longer time periods than other ducks. American wigeon and lesser scaup nest initiations occurred over a shorter period than all other ducks.

The total nesting period was usually shorter during years of drought than during years with wet, warm springs and summers. Warm spring weather with an abundance of surface water areas induced early nesting, whereas extremely hot, dry weather reduced either early or late nesting activities. Furthermore, we believe the nesting period was prolonged more often in years when rainfall occurred frequently and was distributed throughout the nesting season, compared to years of infrequent, light or intense rainfall.

Hatching Chronology and Land Management

Hatch dates for all upland-nesting species during the 16 years varied between 12 May and 12 August (Table 16). Overall mean dates for earliest and latest hatches were 1 June and 2 August, respectively. In the absence of a severe predation problem, much of the hatch curve would be perhaps a month earlier. Length of the hatching season interval varied between 43 and 88 days and averaged 63.

The distribution of potential hatch dates indicated that an average of 43% of the active nests would have been disturbed or destroyed by land-use treatments initiated on 10 July, 33% on 15 July, 22% on 20 July, 15% on 25 July, and 9% on 1 August (Table 16). Furthermore, in 9 of the 16 years, 50% or more of the clutches were still active on 10 July and 25% or more were still active on 15 July. Similarly, Duebbert and Frank (1984) reported that <10% of nests still being incubated would be affected by a mowing date of 21 July.

Vegetation at Nest Sites

The average size of a nest containing a full clutch of eggs, down, and miscellaneous cover is 30 cm in diameter with an area of 706.5 cm^2. Cowardin et al. (1985) stated that a hen probably selects a specific nest site within an area of home range that was selected from the entire breeding range. Why a hen selects a particular nest site is still unknown. We suspect that security has a lot to do with it. Security provided by the vegetation within a meter radius or so of the nest bowl may be critical. Cover may also be a visual relocation cue for the hen during laying and incubation, and for habitat imprint-recognition for the ducklings.

We used a 50% threshold to separate heterogenous vegetation of nest sites into cover classes. For example, if vegetation was a mixture of 40% brush, 5% forbs, and 55% grasses, it was classified as a grassy nest site. At the WSA, 54% of 3,429 clutches (Table 17) were laid in sites concealed by grasses, 18% by forbs, 14% by brush, and 1% by marshy vegetation (marshy vegetation was searched only in dry sites of wetland basins). Blue-winged teal, northern shoveler, and lesser scaup nests occurred

Table 16. *Chronology of hatch dates during 15 years for upland-nesting ducks, Woodworth Study Area, 1967–81.*

Year	*n*	Earliest hatch date	Latest hatch date	Length of hatching season (days)	Percent of unhatched nests before dates				
					10 July	15 July	20 July	25 July	1 August
1967	11	13 June	10 August	59	82	73	46	36	36
1968	24	20 June	5 August	47	83	75	58	50	42
1969	75	16 May	11 August	88	37	28	20	13	9
1970	88	9 June	11 August	64	61	53	43	31	19
1971	114	5 June	12 August	69	62	47	27	22	12
1972	98	1 June	7 August	68	42	39	29	21	12
1973	45	7 June	29 July	53	56	42	27	24	4
1974	122	1 June	8 August	69	57	42	27	22	11
1975	141	1 June	4 August	65	50	43	28	20	13
1976	92	10 June	2 August	54	26	12	4	3	1
1977	70	20 May	31 July	73	30	17	9	3	1
1978	211	12 May	3 August	84	22	18	12	6	4
1979	54	23 May	24 July	63	20	17	9	2	0
1980	26	6 June	18 July	43	50	39	15	0	0
1981	57	28 May	19 July	53	35	19	7	0	0
Total per mean	1,228	1 June	2 August	63	43	33	22	15	9

Table 17. *Percent of upland duck nests occurring by vegetation types, Woodworth Study Area, 1966–81.*

Species	Nests	Vegetation type			
	n	Marsh	Brush	Forb	Grass
Mallard	329	5	21	27	34
Gadwall	611	1	30	33	22
Northern pintail	183	2	14	30	45
Green-winged teal	54	0	33	26	39
Blue-winged teal	1,973	1	8	11	67
Northern shoveler	171	0	4	15	68
American wigeon	55	4	35	31	27
Lesser scaup	53	9	0	8	75
Total	3,429	1	14	18	54

in grassy sites in much greater proportion than other species. Mallards, gadwalls, American wigeon, and green-winged teal nested in brushy sites more readily than other species. Forbs were similarly used by all species except blue-winged teal, northern shovelers, and lesser scaup. Six of eight upland-nesting species used dry marsh sites, but mallards, American wigeon, and lesser scaup used marshes for nesting in proportionately greater frequency than did the other species.

Within stands of seeded nesting cover, 52% of 852 nest sites were in grasses, 45% in forbs, 2% in brush (mostly *Rosa*), and 1% in marshy vegetation. In these stands, mallards, gadwalls, American wigeon, green-winged teal, and northern pintails nested in sites dominated by alfalfa. Blue-winged teal, northern shovelers, and lesser scaup nested predominantly in grassy sites. Within stands of seeded cover, 70% of gadwall nests were in forb sites whereas 70% of the blue-winged teal nests were in grassy sites.

Within stands of native prairie vegetation, 67% of 1,702 nest sites were in grasses, 22% in brush, 9% in forbs, and 2% in marshy vegetation. In these stands, mallards, gadwalls, and American wigeon nested in sites dominated by brush, whereas, the other species nested mostly in grassy sites. Within native prairie, approximately 88% of northern shoveler nests, 85% of lesser scaup nests, 81% of blue-winged teal nests, and 60% of northern pintail nests were in grassy sites. In these stands, 55% of both gadwall and American wigeon nests, and 57% of the mallard nests were in brushy sites.

Of 852 nests in stands of seeded nesting cover, most were associated with the following plant species: alfalfa, 36%; quackgrass (*Agropyron repens*), 11%; smooth brome, 11%; Kentucky bluegrass, 8%; intermediate wheatgrass, 4%; and sweet clover, 3%. With the exception of lesser scaup, nests of all species were more frequently associated with alfalfa than with any other single vegetative species in stands of seeded nesting cover.

Of 1,702 nests found in stands of native prairie, most were associated with the following plant species: Kentucky bluegrass, 29%; wolfberry, 20%; smooth brome, 8%; quackgrass and needlegrass (*Stipa* spp.), 4% each; upland sedges (*Carex* spp.), 3%; and goldenrod (*Solidago* spp.), 2%. Of the nests in native prairie stands, 41% occurred in quackgrass, smooth brome, or Kentucky bluegrass, all of which are introduced cool-season invaders. Kentucky bluegrass was the dominant species at 40% of the blue-winged teal nests and 36% of the northern shoveler nests in native prairie stands. Wolfberry was the dominant species at 50% of the American wigeon nests, 47% of the gadwall nests, 41% of the green-winged teal nests, 36% of the mallard nests, and 21% of the northern pintail nests. In wetlands, *Carex* spp. were the dominant plants at 35% of the lesser scaup nests.

Nest Site Cover Quality, Physiognomy, and Concealment

On the basis of subjective cover quality ratings, 58% of 3,402 nests (Table 18) were in fair nesting cover, 28% in good nesting cover, 7% in excellent nesting cover, and 7% in poor nesting cover. More than 55% of the mallard, gadwall, and American wigeon nests were in good-to-excellent quality cover whereas 50% or more of the blue-winged teal, northern shoveler, and northern pin-

Table 18. *Percent of upland duck nests that occurred in subjectively rated cover, Woodworth Study Area, 1966–81.*

Species	Nests	Cover quality			
	n	Poor	Fair	Good	Excellent
Mallard	324	7	34	42	18
Gadwall	609	1	33	50	16
Northern pintail	183	16	51	24	9
Green-winged teal	53	4	47	36	13
Blue-winged teal	1,958	8	71	18	2
Northern shoveler	169	6	66	27	2
American wigeon	55	2	40	47	11
Lesser scaup	51	4	57	31	8
Total	3,402	7	58	28	7

tail nests were found in poor-to-fair quality cover. Green-winged teal and lesser scaup nests were found in nearly equal proportions in good-to-excellent and poor-to-fair quality cover.

Vegetative cover in the immediate area surrounding nest sites was grouped into eight physiognomic categories (Fig. 16) according to shape of the vegetation actually concealing the clutches. Mallards, gadwalls, American wigeon, northern pintails, lesser scaup, and to a lesser extent, northern shovelers and blue-winged teal selected more nest sites with erect cover and a open or closed canopy than in other sites (Table 19). Brush, forbs, and some of the taller cool-season grasses provided most of the erect cover. Blue-winged teal had more nests in grassy cover, which provided tent-shaped canopies, than the other categories, but they also commonly nested

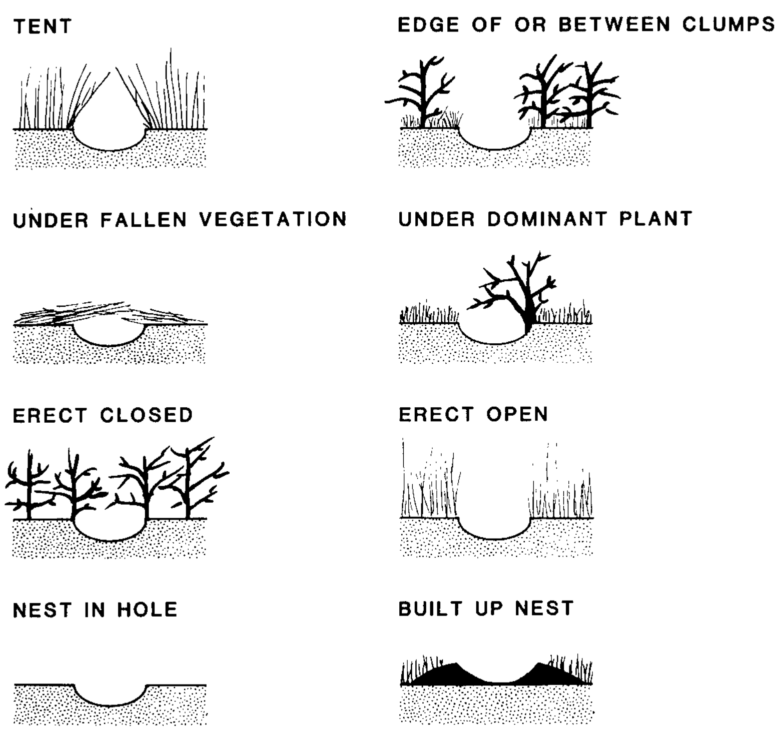

Fig. 16. Each duck nest found was assigned to one of eight categories of nest site type, Woodworth Study Area.

Table 19. *Percent of duck nests found in different types of cover, Woodworth Study Area, 1966–81.*

Species	Nests n	Cover category							
		Tent	Under fallen vegetation	Erect open	Erect closed	Between clumps	Under dominant plant	Built-up nest	Nest in hole
Mallard	302	10	10	36	36	3	5	<1	<1
Gadwall	582	3	5	31	48	6	7	0	1
Northern pintail	168	5	4	65	14	5	5	<1	2
Green-winged teal	49	20	8	18	29	6	18	0	0
Blue-winged teal	1,892	41	7	26	18	2	5	<1	1
Northern shoveler	163	26	12	44	14	2	2	<1	0
American wigeon	53	6	4	21	49	6	15	0	0
Lesser scaup	48	23	10	38	25	2	2	2	0
Total	3,257	26	7	31	26	3	6	<1	1

Table 20. *Percent of upland nests by duck species and top concealment, Woodworth Study Area, 1966–81.*

Species	Nests n	Vegetative top concealment		
		None	Half coverage	Total coverage
Mallard	323	23	48	28
Gadwall	608	20	47	34
Northern pintail	182	51	39	11
Green-winged teal	54	7	48	44
Blue-winged teal	1,972	14	54	32
Northern shoveler	169	23	55	22
American wigeon	55	18	53	29
Lesser scaup	53	11	67	21
Total	3,416	18	52	30

in sites with erect vegetation. Green-winged teal nesting sites were less distinctive in relation to other species, but they nested more in cover that was tented, and erect and under dominant plants, for example, alfalfa.

Nest sites were grouped into three categories according to the amount of vegetation that concealed the top of each nest at the time of discovery: no top concealment, between none and one-half of the nest concealed, and between half and all of the nest concealed. Vegetative cover surrounding the sides of nest sites was grouped into five categories: no concealment, one-fourth concealment, one-half concealment, three-fourths concealment, and complete nest concealment. Except for northern pintails, all species selected sites with top concealment of one-half or greater (Table 20) rather than sites with no top concealment. Northern pintails nested more readily in intensively cultivated fields, where there are more open nesting sites, than did other species (Higgins 1977). These fields provided only sparse, open cover for nesting sites. All species selected nest sites with one-half or greater side concealment (Table 21).

Tradition of Nest Site Selection

With probable over simplification, we submit that the tradition of nest site selection starts with the successful hatching of a clutch. Newly hatched ducklings then have two subjects on which to imprint: the hen (true imprinting) and the vegetative cover (imprint-recognition) immediately sur-

Table 21. *Percent of upland nests by duck species and side concealment, Woodworth Study Area, 1966–81.*

Species	Nests n	Vegetative side concealment None	1/4 nest	1/2 nest	3/4 nest	All nest
Mallard	323	2	2	11	25	59
Gadwall	608	1	1	10	31	59
Northern pintail	182	2	11	25	27	36
Green-winged teal	54	0	2	4	43	52
Blue-winged teal	1,972	1	2	11	30	56
Northern shoveler	169	0	1	16	27	56
American wigeon	55	0	4	13	36	47
Lesser scaup	53	0	0	15	23	62
Total	3,416	1	2	12	30	56

rounding the nest. Brooding may occur for a few hours up to 24 h at the nest. Thus, there is ample time for ducklings to associate with the nest site, after which the brood is usually guided by the hen to a nearby wetland and, subsequently, ducklings are exposed to an ever increasing area of habitat. Ducklings that reach flight stage have usually been exposed to more than one wetland and a rather large area. Movements of mallard and gadwall broods as far as 5.5 km from the nest site were noted by Lokemoen et al. (1984). Beginning with the first flight, ducklings soon become exposed to a greater area on the breeding grounds until they migrate in fall. The following spring, surviving hens attract mates and migrate back to or near where they hatched or to a previously successful nest site, even though extreme drought or other perturbations may have drastically changed the character of these sites.

Evidence of the importance of successful nest sites is borne out in the rates of hens homing back to a particular habitat type or even to the same nest sites (Doty and Lee 1974). During early phases of this study, we became aware that some nest bowls were used in more than 1 year, but we did not know if the reuse of these sites was by the same or different hens. In one instance, the senior author found blue-winged teal nesting in the same nest bowl during 3 consecutive years. The clutch hatched during years 1 and 2 but did not hatch during year 3 and no further nesting occurred at this nest bowl in following years. Reuse of some nest bowls in natural sites has also been reported by Weller et al. (1969), Schamel (1974), and Duebbert et al. (1983), and in nest baskets by Doty and Lee (1974). Duebbert et al. (1983) found that 73% of 252 mallard and 49% of 168 gadwall nests on an island were placed in previously used nest bowls and in six instances, bowls of previously successful nests were reused that same season by later-nesting hens, some of different species. Doty and Lee (1974) found 46% of 113 marked mallard hens homed back to nest baskets and successful hens homed at a significantly ($P < 0.01$) higher rate than unsuccessful hens. In their study, 7 adult hens from 140 web-tagged female ducklings homed and nested in baskets in the vicinity where they were hatched. In brief, adult and juvenile female ducks have an innate ability to home back (Hochbaum 1955) and select a specific nesting site (±30 cm in diameter). The rate of homing is apparently directly related to nest success (whether in natural sites or in human-made baskets). Therefore, recognition or imprint-recognition of nesting site features or any manipulations of nesting habitat that enhance the success of nesting waterfowl are important to waterfowl management.

Clutch Size

Stoudt (1971) demonstrated that unless nest searching was conducted periodically throughout the nesting season, average clutch size figures would be in error because clutches laid later in the season averaged smaller than earlier ones. This was also true at the WSA where average clutch size gradually decreased for all species as the season

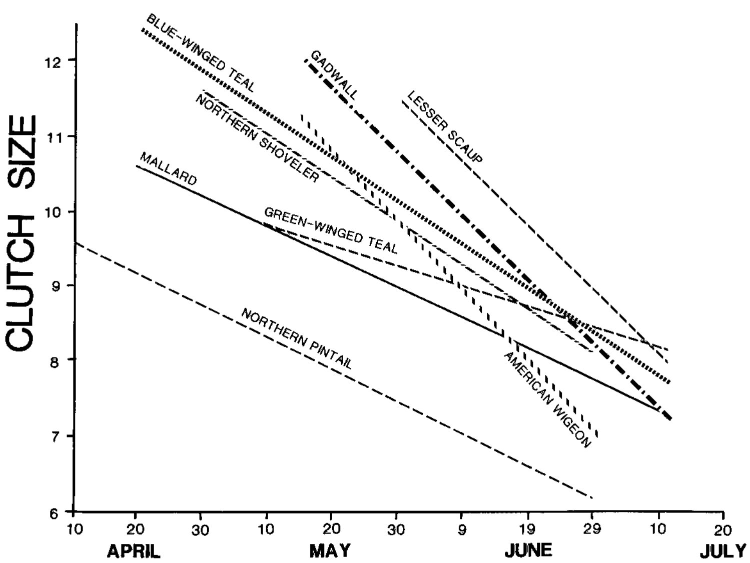

Fig. 17. **Relation of average duck clutch sizes to nest initiation dates, Woodworth Study Area, 1966–81.**

Table 22. *Number and average size of hatched clutches among habitats and species, Woodworth Study Area, 1966–81.*

	Native prairie		Seeded Cover		Cropland		Total	
Species	*n*	$\bar{x}$	*n*	$\bar{x}$	*n*	$\bar{x}$	*n*	$\bar{x}$
Mallard	40	9.4	66	8.9	1	11.0	107	9.1
Gadwall	140	9.9	115	9.8	1	8.0	256	9.9
American wigeon	13	8.3	12	9.2	0	0.0	25	8.7
Green-winged teal	16	8.5	5	9.0	0	0.0	21	8.6
Blue-winged teal	400	10.3	200	10.4	12	9.1	612	10.3
Northern shoveler	32	10.2	30	10.2	0	0.0	62	10.2
Northern pintail	37	8.0	60	7.6	2	10.0	99	7.8
Lesser scaup	14	10.1	2	11.0	1	11.0	17	10.3
Total	692	9.9	490	9.7	17	9.4	1,199	9.8

progressed (Fig. 17). Average seasonal clutch size decreases within species were lesser scaup, 42%; northern pintail, 41%; gadwall, 36%; American wigeon, 35%; blue-winged teal, 32%; northern shoveler, 30%; mallard, 25%; and green-winged teal, 19%. The total average completed clutch size for all species was 29% smaller at the end of the nesting season than it was at the beginning, a substantial reduction in potential duckling production. Nesting later in the season was mainly a contribution from immature or late nesters and renesters, which results from predation, weather, habitat conditions, or combinations of these. Slight variation in mean sizes of hatched clutches was found between nests in native prairie, seeded cover, and cropland habitats and inconsistently among species (Table 22). However, average sizes of hatched clutches for all species inclusive were apparently smaller in burned tracts than in either grazed or idled tracts of native prairie or seeded cover habitats (Table 23). This was expected because nearly all burning was conducted during May and June, which usually eliminated all nesting cover, and with few exceptions, destroyed all active nests. Thus, nearly all successful hatches that occurred during the same year of spring fires would have been late initiations or renests, both of which produce smaller clutch sizes.

Samples of hatched clutch sizes in cropland habitat were small, but the data available indi-

cated a mix of early- and late-laid clutches in standing grain crops and only early-laid clutches in summer fallow (Table 23). Standing crops on the area included both spring- and fall-seeded grain crops. Fall-seeded crops provided early nesting cover whereas spring-seeded crops usually provided mid- to late-season nesting cover. Summer fallow was left uncropped and was tilled several times during the nesting season beginning in late May to early June. Therefore, early-laid clutches had a better chance to hatch.

Nest Failures

Mammalian predators caused 87% of 2,395 nest losses during the study (Table 24); less than 1% was attributed to weather. Most unknown predations probably were caused by either ground squirrels or red fox. Clues to nest predation by these two species are difficult to assess, especially when inspections of nests occur at long intervals.

Destruction of nests by humans and machines was low on this area because only about 12% of the land was annually hayed or cultivated during an average year. On nearby study areas that were 84% or more annually tilled, Higgins (1977) found 19% of the nest destruction was caused by men and machines, and on the cropland portion farm machinery destroyed 93% of active nests during tillage operations.

We found it difficult to assign nest loss to a specific predator. Of 2,374 nest failures, the specific predator causing a failure was attributed at only 1,595 (67%) of the destroyed nests. Most (64%) predation nest failures were caused by red fox. Mink, weasels, and cattle trampling caused less than 1% (Table 25).

Predation by badgers, raccoons, and gulls was fairly consistent throughout the study whereas predation by red fox, skunks, and ground squirrels varied greatly among years. Although we had no definite means of enumerating these species, the frequency that they were seen and annually trapped by the public, suggested that the amount of predation by these three species was largely related to their densities.

Overall Duck Nest Densities, Success, and Production

The density of 3,821 duck nests on 8,464 ha of searched uplands averaged 45/km^2. This calculated to an average annual density of 0.07 nest per hectare or 2.2 ha per nest during 1966–81. Nest success for 3,517 nests with complete histories averaged 16.3% Mayfield. In all, 11,430 duck eggs hatched, yielding an annual average of 1 duckling per 0.7 ha or 55.6 ducklings per 40.5 ha of upland cover.

Duck nest success did not differ among species for all years combined (χ^2 = 13.1, 7 df, P = 0.70; Table 26), but it did differ among years for all species in combination (χ^2 = 122.0, 15 df, P = 0.001; Table 27).

Effects of Cover Height

Significantly greater duck nest success occurred as cover increased in height, or conversely, predation was significantly reduced by taller vegetative cover at nest sites (Kirsch et al. 1978). Cover height effect, even though significant overall, was not constant among duck species. Our data showed that as cover height increased, the daily mortality of nests decreased for mallards, gadwalls, and northern shovelers; remained the same for blue-winged teal and green-winged teal; and increased for northern pintails (Fig. 18). Possibly the high proportion of blue-winged teal among the duck population during recent years is related, in part, to the fact that their nest success is independent of cover height. Meltofte (1978), Duebbert and Lokemoen (1980), and Lokemoen et al. (1984) reported ducks used nest sites with taller and denser cover even when predation rates were low. Our results are in general agreement with those of Heiser (1971); Dwernychuk and Boag (1972); Kirsch et al. (1978); Livezey (1981a, 1981b); and Hines and Mitchell (1983).

Using part of our data (1974–76), Kirsch et al. (1978) showed a direct relation between nest densities, as well as nest success for five species of upland-nesting ducks, and readings of visual obstruction along transects in cover fields before new spring growth affected readings in the residual cover. Height and density of vegetative cover at the nest sites, throughout the season, and of total residual cover in early spring before new growth, are important to duck nest success and nest densities.

Effects of Habitat Type

Waterfowl populations fluctuate in the Missouri Coteau as habitats change due to annual moisture

Table 23. *Number of duck nests and average size of successfully completed clutches among treatments within habitats by species, Woodworth Study Area, 1966–81.*

Habitat and treatment	Mallard		Gadwall		American wigeon		Green-winged teal		Blue-winged teal		Northern shoveler		Northern pintail		Lesser scaup		Total	
	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$
Native prairie																		
Burned	2	9.5	18	9.4	4	8.0	3	8.5	48	9.8	2	9.8	1	8.0	1	11.0	79	9.6
Grazed	5	9.6	32	10.0	0	—[a]	5	9.3	88	10.1	1	10.0	5	7.9	3	11.0	139	9.9
Idle	34	9.2	94	9.9	9	8.7	9	8.9	274	10.4	30	10.2	32	7.8	10	9.5	492	9.9
Seeded cover																		
Burned	2	7.8	11	9.7	1	10.0	0	—	9	10.5	1	10.0	2	8.0	0	—	26	9.8
Idle	67	8.8	105	9.7	11	9.2	4	9.5	189	10.3	27	10.1	57	7.6	3	11.0	463	9.6
Cropland																		
Standing crop	0	—	1	8.0	0	—	0	—	7	8.1	0	—	1	11.0	1	11.0	10	8.7
Stubble	0	—	0	—	0	—	0	—	1	6.0	0	—	0	—	0	—	1	6.0
Mulched stubble	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—	0	—
Summer fallow	1	11.0	0	—	0	—	0	—	2	11.5	0	0.0	1	9.0	0	0.0	4	10.8

[a] — Indicates no data.

Table 24. *Summary of causes of duck nest losses, Woodworth Study Area, 1966–81.*

Species	Losses (n)	Mammal	Bird	Unknown predators	Human–machine	Weather	Fire	Unknown causes
Mallard	262	225	8	8	1	4	12	4
Gadwall	384	341	6	17	11	1	1	7
American wigeon	35	33	1	0	0	0	0	1
Green-winged teal	33	30	1	1	1	0	0	0
Blue-winged teal	1,409	1,237	28	58	36	0	28	22
Northern shoveler	119	95	2	9	7	0	5	1
Northern pintail	120	101	4	8	5	0	1	1
Lesser scaup	33	29	1	1	1	0	0	1
Total	2,395	2,091 (87%)	51 (2%)	106 (4%)	69 (3%)	2 (<1%)	39 (2%)	37 (2%)

regimes. The amount of precipitation that comes before and during the growing season influences growth of upland vegetation and water levels in potholes.

There were four broad types of upland-nesting habitats on the area: marshy vegetation in dry wetlands, annually tilled croplands including summer fallow, native mixed-grass prairie, and former croplands currently sown to mixtures of cool-season grasses and legumes. All upland habitat classes were used for nesting by all species of upland-nesting ducks at some time during the study. The small sample of nests (33) in dry wetlands, averaging only about three per year and consisting primarily of mallards, gadwalls, and lesser scaup, curtailed further comparisons among years and species for this habitat. Most duck nesting is completed by the time most basins dry up; which probably accounts for the infrequent occurrence of duck nesting in dry wetland basins. Thus, we include comparisons only of croplands, native prairie, and seeded grassland habitats in the remainder of this report.

Although duck nesting success averaged slightly higher in seeded grasslands (18%) than in native prairies (16%) or croplands (13%; Table 28), nest success did not differ ($\chi^2 = 0.02$, 1 df, $P > 0.90$) significantly between seeded and native prairie habitats for all species and years combined, but it differed significantly among years ($\chi^2 = 134.3$, $P < 0.001$); interactions between years and habitats were not significant (Table 28). Nest success

Table 25. *Probable causes of upland nest losses among ducks, Woodworth Study Area, 1966–81.*

Species	Red fox	Striped skunk	Ground squirrel	Gull	Raccoon	Badger	Mink–weasel	Cow
Mallard	91	20	17	6	12	3	2	0
Gadwall	167	52	18	6	13	14	1	0
American wigeon	18	4	0	1	1	1	0	0
Green-winged teal	8	8	1	1	1	1	0	0
Blue-winged teal	610	260	33	21	23	6	0	3
Northern shoveler	57	19	3	1	0	0	0	0
Northern pintail	51	9	6	4	1	3	0	0
Lesser scaup	11	5	0	0	2	0	0	0
Total	1,013 (64%)	377 (24%)	78 (5%)	40 (3%)	53 (3%)	28 (2%)	3 (<1%)	3 (<1%)

Table 26. *Upland nest success by duck species for all years combined, Woodworth Study Area, 1966–81.*

Species	Nests found (*n*)	Nests hatched (*n*)	Percent apparent success	Daily mortality rate	Percent Mayfield success[a]
Mallard	367	109	30.0	0.0545	14.9
Gadwall	654	264	40.4	0.0440	21.7
Northern pintail	225	100	44.4	0.0516	16.5
Green-winged teal	56	22	39.3	0.0532	15.6
Blue-winged teal	1,925	607	31.5	0.0548	14.7
Northern shoveler	181	63	34.8	0.0519	16.3
American wigeon	58	25	43.1	0.0430	22.4
Lesser scaup	51	18	35.3	0.0550	14.6
Total	3,517	1,208	34.4	0.0521	16.3

[a] Nest success among species did not differ significantly ($\chi^2_7 = 13.1$, $P > 0.05$).

Table 27. *Nest success by years (n = 16) for all upland-nesting duck species, Woodworth Study Area, 1966–81.*[a]

Year	Number of nests: Found	Destroyed	Hatched	Percent apparent success	Percent Mayfield success
1966	38	34	4	10.5	4.6
1967	117	106	11	9.4	4.4
1968	137	113	24	17.5	7.2
1969	145	70	75	51.7	27.6
1970	279	189	90	32.2	11.3
1971	225	109	116	51.6	28.1
1972	352	254	98	27.8	10.9
1973	183	138	45	24.6	9.3
1974	311	188	123	39.5	19.4
1975	429	287	142	33.1	15.9
1976	359	267	92	25.6	11.9
1977	151	81	70	46.4	22.8
1978	418	207	211	50.5	30.3
1979	140	86	54	38.6	22.8
1980	90	64	26	28.9	12.1
1981	143	86	57	39.9	21.5
Total	3,517	2,279	1,238	35.2	16.3

[a] Nest success among years varied significantly ($\chi^2_{15} = 122.0$, $P < 0.05$).

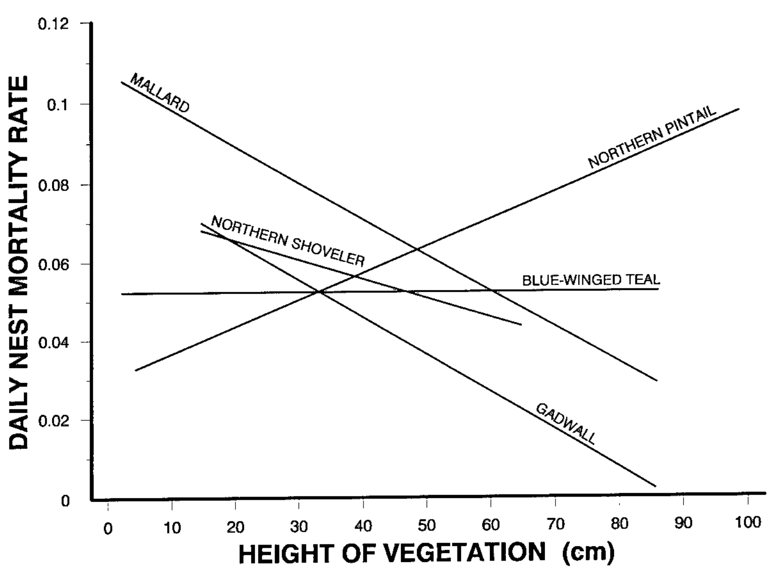

Fig. 18. Relation of the daily mortality rates in relation to height of vegetation of duck nests by species, Woodworth Study Area, 1973–81.

did not differ significantly among field size classes ($\chi^2 = 4.6$, 3 df, $P > 0.10$; Table 29).

Ducks nested in greater densities in seeded grasslands (33 nests per 40.5 ha) than in native mixed-grass prairie (16 nests per 40.5 ha), or in annually tilled croplands (about 3 nests per 40.5 ha; Table 30). For all species and habitats combined, the average annual nest density during 1966–81 was 18.2 nests per 40.5 ha, or 45 nests per square kilometer. All species except lesser scaup showed the highest nest densities in seeded grasslands (Table 31). Lesser scaup had slightly greater

Table 28. *Nest success in three major habitats for all duck species and years, Woodworth Study Area, 1966–81.*[a]

Habitat	Number of nests: Found	Destroyed	Hatched	Percent apparent success	Percent Mayfield success
Seeded grasslands	1,366	849	501	36.7	17.7
Native prairie	2,081	1,371	710	34.1	15.7
Croplands[b]	60	40	20	33.3	12.5
Total	3,507	2,260	1,231	35.2	16.3

[a] Nest success varied among years (χ^2_{13} = 134.3, $P > 0.001$) but not between seeded grasslands and native prairie (χ^2_1 = 0.02, $P > 0.90$). Interaction between years and habitats was not significant (χ^2_{13} = 11.01, $P > 0.25$).

[b] Categories not included in tests for year and habitat effects because of small or incomplete samples; also, nest data were not available for native prairie in 1979 or 1980.

nest densities in native prairie habitat, particularly, near wetland margins, than in seeded grassland (0.3 vs. 0.2 nests per 40.5 ha). We did not find any nests of American wigeon or green-winged teal in annually tilled croplands. Nest densities were much greater in fields of smaller size (Table 29) for all habitat types.

Among habitat types, annual duckling production was greater in seeded grasslands (100 ducklings per 40.5 ha) than in native prairie (35 ducklings per 40.5 ha), or in annually tilled croplands (7 ducklings per 40.5 ha; Table 30).

We had complete histories on 2,081 nests found in native mixed-grass prairie during 16 years of searches. Plant communities were numerous within this habitat type and seldom distinct from one another. For example, the potential natural vegetation community for the area is *Agropyron–Stipa–Andropogon* (Küchler 1964), but it was often invaded by Kentucky bluegrass, smooth bromegrass, buckbrush, silverberry, and quackgrass or combinations of these.

Dix and Smeins (1967) classified the native mixed-grass prairie into high prairie, mid-prairie, and low prairie. Relative to these classes, we found few duck nests in high prairie, low numbers in low prairie, and high numbers in mid-prairie. In general, native mixed-grass prairie provided the greatest diversity of nesting sites among the four nesting habitats.

Higgins (1981) reported that 37,864 ha of native prairie occurred on 1,746 federal waterfowl production areas in five states in the glaciated prairie pothole region. Based on a density of 34.5 ducklings per 40.5 ha from our study, the U.S. Fish and Wildlife Service could hatch 32,239 ducklings per year from these areas; however, the potential is much higher with lower predation effects.

The complete histories on 1,366 nests found in seeded grasslands were used as data. The nesting cover among fields in this type was similar except when sweetclover became dominant, which was usually during the second growing season (Higgins and Barker 1982). On average, seeded grasslands were the most productive nesting habitat on the WSA. In other studies, seeded grasslands also supported high densities of nesting ducks relative to other cover types (Duebbert 1969; Miller 1971; Oetting and Cassel 1971; Duebbert and Kantrud 1974; Nelson and Duebbert 1974; Duebbert and Lokemoen 1976; Cowardin and Johnson 1979; Livezey 1981a, 1981b).

Most nesting in cropland on the WSA was in standing, small-grain crops rather than stubble or summer fallow. Cowardin et al. (1985) analyzed mallard preferences for nesting among available habitats on a nearby study area and found mallards nested in croplands less than expected relative to its availability. Our data agree with their results for all upland-nesting species.

Effects of Land-use Treatments

Land-use treatments apparently affected nest success more than the habitat types. Among land-use treatments within native prairie, duck nesting success averaged higher in burned fields (18.3%) than grazed pastures (13.0%) or idle fields (12.9%), but the difference was not significant

Table 29. *Percent Mayfield nest success (numbers of nests in parentheses) and nest density (nests per 40.5 ha) by field size class and year, Woodworth Study Area, 1966–81.*

Year	Size classes of fields (ha)				
	<4	4–16	8–16	16–32	>32[b]
Mayfield nest success[a]					
1966[b]	4.7 (37)	—[c] (0)	— (0)	— (0)	— (0)
1967	4.7 (15)	3.8 (15)	4.6 (31)	4.3 (57)	— (0)
1968	2.4 (14)	13.5 (15)	7.0 (61)	10.5 (34)	2.1 (13)
1969	25.5 (13)	26.7 (25)	37.1 (67)	17.8 (41)	— (0)
1970	6.9 (30)	12.1 (42)	13.4 (63)	17.1 (56)	8.1 (90)
1971	34.9 (28)	16.4 (20)	32.9 (59)	39.9 (30)	24.2 (87)
1972	8.2 (27)	9.1 (44)	9.0 (77)	9.7 (65)	14.0 (136)
1973	4.2 (13)	14.3 (27)	7.3 (55)	5.4 (17)	11.7 (71)
1974	19.5 (25)	30.8 (50)	14.3 (61)	17.9 (40)	18.3 (136)
1975	15.6 (26)	16.4 (72)	23.2 (83)	18.7 (48)	12.7 (201)
1976	16.9 (22)	5.8 (64)	10.6 (83)	9.0 (55)	17.5 (129)
1977	18.0 (10)	10.8 (24)	34.8 (49)	10.7 (26)	30.0 (40)
1978	28.8 (29)	29.1 (65)	33.0 (143)	13.2 (53)	37.6 (128)
1979	43.2 (4)	9.2 (18)	28.8 (81)	16.9 (34)	— (0)
1980	14.7 (8)	9.7 (17)	15.3 (48)	6.0 (16)	— (0)
1981	31.6 (6)	6.4 (14)	16.0 (25)	32.8 (18)	24.7 (78)
Total	13.4 (307)	14.7 (512)	18.7 (986)	13.3 (590)	17.8 (11,109)
Mayfield nest densities					
1966	—	—	—	—	—
1967	150	38.8	39.8	45.2	—
1968	929	32.1	62.0	27.3	53.1
1969	235	37.4	49.1	20.8	—
1970	178	69.5	46.2	26.9	34.2
1971	88.8	40.4	27.4	11.3	22.3
1972	70.4	64.1	50.3	35.5	36.1
1973	102	30.8	39.6	8.7	20.7
1974	77.6	27.8	36.7	22.2	33.2
1975	59.0	76.0	37.8	27.6	49.8
1976	91.1	77.4	37.5	43.4	28.9
1977	60.1	30.9	18.1	24.3	9.9
1978	77.8	57.8	51.5	32.7	26.2
1979	57.9	85.7	113	152	—
1980	85.2	109	101	116	—
1981	73.1	43.6	27.5	15.8	17.1
Total	114	50.8	43.3	28.5	27.8

[a] Nest success varied among years (χ^2_{14} = 127.7, P <0.001) but not among field size classes (χ^2_{3} = 4.6, P >0.10). The interaction was not significant (χ^2_{42} = 43.3, P >0.25).

[b] Category not used in analysis because of incomplete data.

[c] No data.

Table 30. *Densities of upland nests and ducklings hatched in three habitats, Woodworth Study Area, 1966–81.*

Habitat	Ha searched	Nests found	Nest density (nests per 40.5 ha)	Eggs hatched	Ducklings per 40.5 ha
Native prairie	5,801	2,292	16.2	6,692	47.3
Seeded grasslands	1,787	1,455	33.4	4,585	105.2
Croplands	877	74	3.5	153	7.2
Total	8,464	3,821	18.5	11,430	55.3

Table 31. *Apparent upland duck nest densities for three habitat types, Woodworth Study Area, 1966–81.*

	Nest densities (nests per 40.5 ha)			
Species	Native prairie (5,801 ha)	Seeded grasslands (1,787 ha)	Annually tilled croplands (877 ha)	Average
Mallard	1.2	5.2	0.4	1.9
Gadwall	3.7	7.0	0.4	4.1
Northern pintail	0.7	2.9	0.4	1.1
Green-winged teal	0.3	0.4	0.0	0.3
Blue-winged teal	10.0	14.5	1.6	10.1
Northern shoveler	0.7	1.9	0.2	0.9
American wigeon	0.2	0.6	0.0	0.3
Lesser scaup	0.3	0.2	0.1	0.2

(χ^2 = 2.35, 2 df, P = 0.309) nor consistent among species (Table 32). Another analysis comparing nest success among land-use treatments within years yielded a marginally significant effect. Except for blue-winged teal and gadwalls, ducks experienced lower nest success in grazed pastures. In grazed pastures, gadwalls nested predominantly in wolfberry patches that generally offer taller and denser cover than other pasture sites. American wigeon, green-winged teal, blue-winged teal, northern shovelers, and lesser scaup had the highest nest success in burned native prairie, but mallards had the best success in idle native prairie (Table 32). Northern pintails had nearly equal nest success in burned or idle native prairie and were least successful in grazed pastures.

Among land-use treatments of seeded grasslands, nest success was higher in burned (22.7%) than idle (16.7%) or grazed (9.3%) fields. Among duck species and treatments within seeded grasslands, nest success was highest in burned fields for all species except mallards, northern shovelers, and northern pintails; mallard nest success in burned fields was nearly equal that of idle fields.

We suggest that duck nest success and densities in seeded grasslands could be enhanced by treatment with fire at 3–4 year intervals. We burned seeded grasslands during March–June; however, we achieved best plant regrowth with burns in March and April, and weather permitting, also in May for the cool-season grass–alfalfa mixtures in our plantings. Early spring burns allowed total field restoration and regrowth during the burn year and a longer fire-free nesting and renesting interval after the fire event in the burn year.

Among land-use treatments in annually tilled croplands, nest success was greater in standing grain crops (20.7%) than in summer fallow (12.5%), mulched stubble (3.7%), or standing stubble (2.3%). Except for blue-winged teal, nest samples among species and treatments were too small for

meaningful comparisons of nest success rates among species. Blue-winged teal had their highest nest success in growing grain.

In seeded grasslands, nest densities were greater in idle cover (46.3 nests per 40.5 ha) than burned fields (22.8 nests per 40.5 ha) or grazed fields (17.8 nests per 40.5 ha; Table 33). Nest densities were greater in idle cover than in burned or grazed cover for all species except lesser scaup.

Within native prairie, nest densities were greater in idle fields (26.7 nests per 40.5 ha) than grazed pastures (15.7 nests per 40.5 ha) or burned fields (14.7 nests per 40.5 ha).

In annually tilled cropland, nest densities were greater in summer fallow (5.2 nests per 40.5 ha) and standing green crops (4.2 nests per 40.5 ha) than mulched (2.7 nests per 40.5 ha) or standing stubble (1.0 nests per 40.5 ha). These density results are in general agreement with earlier results reported by Higgins (1977).

Within native prairie, duckling production was greater in idle fields (70.7 ducklings per 40.5 ha) than burned fields (46.8 ducklings per 40.5 ha) or grazed pastures (40.7 ducklings per 40.5 ha; Table 34). Duckling production averaged higher in idle fields of native prairie than grazed or burned fields for all duck species except American wigeon.

In seeded grasslands, duckling production was higher in idle cover (141.5 ducklings per 40.5 ha) than burned (83.9 ducklings per 40.5 ha) or grazed fields (22.0 ducklings per 40.5 ha).

Duckling production averaged higher in summer fallow fields (20.8 ducklings per 40.5 ha) than in growing grain crops (8.9 ducklings per 40.5 ha) or standing stubble (0.9 duckling per 40.5 ha). No ducklings hatched from fields of stubble mulch. The high number of cropland fields with no nests, or in which no ducklings hatched, prevented comparing duckling production among species by land-use treatments within croplands.

The eight species of upland-nesting ducks used fields of native mixed-grass prairie regardless of whether the fields were burned, grazed, or idled. Gadwalls, American wigeon, green-winged teal, and blue-winged teal had average nest success rates ≥15% in burned treatments, whereas only gadwalls and green-winged teal had such rates in grazed pastures. In idled fields, gadwalls, American wigeon, green-winged teal, blue-winged teal, northern shovelers, northern pintails, and lesser scaup all had average nest success rates ≥15%.

Few studies have been conducted in these same habitats on the effects of fire on habitats and subsequent production of nesting ducks. Fritzell (1975) reported lower densities of duck nests on burned cover (0.5 nest per hectare) than on unburned cover (1.2 nest per hectare), but higher apparent nest success in burned cover (38.5%) than in unburned cover (15.0%) during a 2-year study in southern Manitoba. Kirsch and Kruse (1973) similarly reported a higher apparent success for duck nests on burned grasslands during the second growing season after a fire (52%) than on undisturbed (33%) or grazed areas (23%). Their results were based on the analysis of the 1966–71 portion of this data. Nest success rates observed by them on burned areas were higher than the overall apparent nest success rates on burned areas for the years 1966–81 (52 vs. 34%).

All species of upland-nesting ducks used seeded grassland habitat regardless of land-use treatment, except for American wigeon and green-winged teal, two species that were sparsely distributed in the WSA. Mallards, gadwalls, northern pintails, American wigeon, blue-winged teal, and northern shovelers had average nest success rates ≥15% in nonused fields of seeded grassland, whereas in burned fields only mallards, gadwalls, American wigeon, and blue-winged teal had average rates ≥15%, and in grazed areas none had average rates ≥15%.

Several studies have been conducted on duck nesting in seeded grasslands of the types we studied, but few have dealt with the effects of land-use treatments on duck production in seeded grasslands. Livezey (1981a) compared duck nesting among land-use treatments in seeded grasslands at Horicon NWR in Wisconsin and reported that mowing and haying significantly reduced duck nest densities until the second year after mowing, when fields seemed fully restored to pretreatment vegetation structure. He also found duck nest densities and success to be similar among hayed fields and long-retired fields (5+ years). Our results relative to treatments are in agreement with Livezey (1981a) in that the effects reduced duck nesting during the treatment year and the subsequent year, particularly with burning treatments.

Table 32. *Percent of upland nest success among treatments in habitats by duck species, Woodworth Study Area, 1966–81.*[a]

Habitat and treatment	Mallard		Gadwall		Northern pintail		Green-winged teal		Blue-winged teal		Northern shoveler		American wigeon		Lesser scaup		Total	
	n	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
Native prairie																		
Burned	98	10.2	184	24.0	49	21.3	8	25.7	750	17.2	59	22.3	19	29.8	20	25.4	1,187	18.3
Grazed	18	12.8	79	25.5	22	4.0	14	16.4	330	12.3	19	3.6	2	2.6	10	9.1	494	13.0
Idle	50	17.9	98	17.1	26	21.7	19	19.1	360	10.3	26	19.8	10	13.1	7	20.0	596	12.9
Seeded cover																		
Burned	24	16.2	58	31.4	12	13.1	1	100.0	107	21.5	14	7.0	3	54.5	4	11.8	223	22.7
Grazed	2	3.7	1	2.4	1	100.0	0	0.0	14	4.4	1	100.0	0	0.0	2	3.4	21	9.3
Idle	201	16.8	250	18.7	115	19.0	13	5.6	507	15.5	70	17.7	25	20.5	5	3.6	1,186	16.7
Cropland																		
Standing crop	4	2.5	7	55.5	5	5.5	0	0.0	18	33.8	3	3.2	0	0.0	2	25.0	39	20.7
Stubble	0	0.0	0	0.0	2	1.3	0	0.0	5	2.9	0	0.0	0	0.0	0	0.0	7	2.3
Mulched stubble	1	3.7	1	2.8	0	0.0	0	0.0	3	4.7	0	0.0	0	0.0	0	0.0	5	3.7
Summer fallow	3	11.8	0	0.0	2	37.5	0	0.0	6	6.4	0	0.0	0	0.0	1	1.0	12	12.5

[a] Percent nest success is by the Mayfield method.

Table 33. *Apparent density of upland duck nests (nest per 40.5 ha) among treatments in habitats by species, Woodworth Study Area, 1966–81.*

Habitat and treatment	Ha searched	Mallard	Gadwall	Northern pintail	Green-winged teal	Blue-winged teal	Northern shoveler	American wigeon	Lesser scaup	Total
Native prairie										
Burned	3,279	1.20	2.27	0.60	0.10	9.26	0.73	0.23	0.25	14.65
Grazed	1,273	0.57	2.51	0.70	0.45	10.49	0.60	0.10	0.32	15.70
Idle	902	2.24	4.39	1.17	0.85	16.14	1.17	0.45	0.31	26.73
Seeded cover										
Burned	397	2.45	5.92	1.22	0.10	10.92	1.43	0.31	0.41	22.76
Grazed	48	1.69	0.85	0.85	0.0	11.86	0.85	0.0	1.69	17.80
Idle	1,037	7.84	9.75	4.49	0.51	19.78	2.73	0.98	0.20	46.27
Cropland										
Standing crop	376	0.40	0.80	0.50	0.0	1.90	0.30	0.0	0.20	4.20
Stubble	285	0.0	0.0	0.30	0.0	0.70	0.0	0.0	0.0	1.00
Mulched stubble	75	0.50	0.50	0.0	0.0	1.60	0.0	0.0	0.0	2.70
Summer fallow	85	1.30	0.0	0.90	0.0	2.60	0.0	0.0	0.40	5.20

Table 34. *Average ducklings hatched (ducklings per 40.5 ha) in habitat treatments by species, Woodworth Study Area, 1966–81.*

Habitat and treatment	Ha searched	Mallard	Gadwall	Northern pintail	Green-winged teal	Blue-winged teal	Northern shoveler	American wigeon	Lesser scaup	Total
Native prairie										
Burned	3,279	2.10	9.22	1.95	0.38	28.92	2.44	0.99	0.88	46.86
Grazed	1,273	1.37	9.60	0.95	1.11	26.26	0.32	0.0	1.05	40.65
Idle	902	6.82	12.38	4.39	2.91	37.22	4.62	0.94	1.39	70.67
Seeded cover										
Burned	397	6.53	28.57	4.80	1.02	35.61	4.18	2.04	1.12	83.88
Grazed	48	0.0	0.0	7.63	0.0	6.78	7.63	0.0	0.0	22.03
Idle	1,037	19.47	30.67	15.02	1.05	62.04	9.48	3.32	0.43	141.47
Cropland										
Standing crop	376	0.0	0.86	0.86	0.0	6.02	0.0	0.0	1.18	8.93
Stubble	285	0.0	0.0	0.0	0.0	0.85	0.0	0.0	0.0	0.85
Mulched stubble	75	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Summer fallow	82	4.9	0.0	4.42	0.0	11.36	0.0	0.0	0.0	20.83

Sample sizes for individual duck species were small among treatment divisions within annually tilled cropland. However, there was one obvious difference among ducks nesting in the cropland treatments. Fields of standing grain were used by all species of upland-nesting ducks except American wigeon and green-winged teal, and were comparatively more attractive and productive to ducks than fields of stubble or summer fallow. Winter rye provided earlier standing grain cover than did spring-seeded wheat, barley, or oats. Winter wheat was not available during this study but became available as a potentially good nesting cover crop during the 1980's. Gadwalls, blue-winged teal, and lesser scaup nested with better success in growing grain (55.5, 33.8, and 25.0%, respectively) than did northern pintails, northern shovelers, or mallards (5.5, 3.2, and 2.5%, respectively). This was probably because the former three species are mid-to-late nesters and growing grain is taller and denser later in the year.

Generally, our results relative to annually tilled croplands were in agreement with results reported by other duck studies (Milonski 1958; Moyle 1964; Evans and Wolfe 1967; Smith 1971; Stoudt 1971; Higgins and Kantrud 1973; Duebbert and Kantrud 1974; Higgins 1977; Cowan 1982). Further, we think annually tilled croplands will give greater duck production when a substantial proportion of this habitat type within the prairie pothole region is managed for winter wheat and winter rye, or is under minimum or no-till cultivation systems. A study by Cowan (1982) comparing nest success in zero tillage and conventional tillage grain cropping supports our belief.

Estimates of Duck Production

Brood Census Periods

Two brood counts were made each year except in 1978 when only one was made. Usually the initial count was begun when broods were first seen in Age Class II-A (Gollop and Marshall 1954), between 25 June and 15 July, and the second count was made between 25 July and 15 August. We think that estimates of the overall brood production are best based on two field counts because species have different hatching dates. Incidental sightings of Class I age broods between the July and August counts, and after the August count, can be used either to augment the total brood count or to eliminate duplication of broods already counted during earlier regular counts, using cross-matching broods by age, species identification, brood size, and location. This method of brood censusing and tallying takes considerable field effort by several people each year, possibly 40 work hours per 200 wetlands for two censuses and 2 work hours per 200 wetlands to tally and remove duplicate brood sightings between counts and between counts and incidental sightings. Overall, we believe this method gave us a fairly reliable estimate of the total duck production.

Number of Broods

The number of duck broods estimated on the study area each year varied from 47 to 301 during 1965–81 and averaged 148 (Table 35). The two highest counts of broods occurred in 1966 and 1969. These were years of below average total precipitation and above average winter snowfall. From 2 to 5 March 1966, an estimated 76 cm or more of snow accumulated during a severe blizzard and at least 122 cm of snow accumulated during the winter of 1968–69.

The lowest number of broods was censused in 1973, a year of near-average total precipitation but below-average winter snowfall. As with pairs, there was no direct correlation between the number of broods and the total amount of annual precipitation.

Brood counts are only an index to production because they are affected by the same wetland and climatic conditions that affect pair counts. In addition, accuracy of counts is influenced by behavioral characteristics of hens seeking shelter and protection for broods and by the movements of broods between wetlands. We assumed that with brood movements on a block study area, ingress equaled egress.

Pond Occupancy by Broods, Species Composition of Broods, and Brood Densities

During 1965–75, the percent of wetland basins occupied by broods of all species varied from 11–36% and averaged 17% for July censuses. In August, the percent varied from 14–50% and averaged 20%. Generally, percent occupancy of wet basins by broods increased as the number of wet basins decreased during late summer. Broods,

Table 35. *Minimum number of duck broods, Woodworth Study Area, 1965–81.*

Species	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	Range	Total	$\bar{x}$
Dabbling ducks																				
Mallard	9	26	8	2	23	12	20	11	4	10	20	3	19	14	9	10	20	2–26	220	13
Gadwall	27	39	15	16	34	13	35	14	5	33	13	17	25	17	11	22	14	5–39	350	21
Northern pintail	20	13	5	5	22	5	2	3	2	13	6	2	3	3	6	3	2	2–22	115	7
Green-winged teal	5	9	7	4	4	3	7	1	1	3	2	0	0	2	0	1	0	0–9	49	3
Blue-winged teal	77	165	131	77	147	67	92	73	30	50	119	12	26	55	72	30	27	12–165	1,250	74
Shoveler	12	16	13	5	19	8	4	8	2	4	6	1	2	7	7	5	1	1–19	120	7
American wigeon	5	5	1	2	4	3	8	4	0	4	1	0	2	4	5	3	7	0–8	58	3
Total dabbling ducks	155	273	180	111	253	111	168	114	44	117	167	37	80	104	111	74	71	37–273	2,170	128
Diving ducks																				
Redhead	8	2	2	3	3	4	2	2	0	8	4	6	0	2	2	11	3	0–11	62	4
Canvasback	2	4	1	0	1	3	0	1	1	5	2	4	0	1	11	5	13	0–13	54	3
Lesser scaup	5	6	0	3	9	5	7	5	0	1	3	2	0	5	0	8	13	0–13	72	4
Ruddy duck	9	14	10	2	8	5	2	3	0	11	20	25	0	10	1	5	5	0–25	130	8
Ring-necked duck	0	2	1	0	2	0	0	0	0	0	0	2	0	0	0	1	0	0–2	8	0.5
Total diving ducks	24	28	14	8	23	17	11	11	1	25	29	39	0	18	14	30	34	1–39	326	19
Unidentified	0	0	0	2	4	0	3	5	2	1	0	0	1	0	3	0	5	0–5	26	2
Total	179	301	194	121	280	128	182	130	47	143	196	76	81	122	125	104	110	47–301	2,519	148

Table 36. *A comparison of species composition of all duck broods and estimated pairs, Woodworth Study Area, 1965–81.*

Species	Percent species composition averaged for 17 years: Estimated pairs	All broods and indicated broods
Dabbling Ducks		
Mallard	11	9
Gadwall	14	14
Northern pintail	6	5
Green-winged teal	2	2
Blue-winged teal	46	50 [a]
Northern shoveler	6	5
American wigeon	2	2
Total dabbling ducks	86	86
Diving Ducks		
Redhead	4	3
Canvasback	1	2 [a]
Lesser scaup	5	3
Ring-necked duck	<0.5	<0.5
Ruddy duck	4	5 [a]
Total diving ducks	14	14

[a] Brood estimates higher than their respective pair estimates may be the result of counting ability or brood immigration onto the area.

more than pairs, tended to congregate on certain wetlands but avoided others. This tendency was apparent during consecutive years.

During 1965 through 1981, dabbling duck broods averaged 86% and diving ducks 14% of the brood populations, the same proportions as with pair populations (Table 36).

Blue-winged teal were the most abundant species in all years, averaging 46% of the pair population and 50% of total broods in July plus August counts.

Brood densities per 2.6 km^2, from 1965 through 1981, varied from 10 to 63, and averaged 31 (0.02 broods per hectare), in an area of 19% wetlands and 81% uplands. Mean brood densities per 2.6 km^2 per species for this same period were blue-winged teal, 16; gadwalls, 4; mallards, 3; ruddy ducks, 2; American wigeon, canvasbacks, green-winged teal, lesser scaup, northern pintails, northern shovelers, redheads, 1 each; and ring-necked ducks, ≤1. Highest brood densities by species were blue-winged teal, 35; gadwalls, 8; mallards and northern pintails, 5; northern shovelers and ruddy ducks, 4; canvasbacks, 3; American wigeon, green-winged teal, lesser scaup and redheads, 2; and ring-necked ducks, ≤1.

The relation of brood densities to wetland size was generally different between diving duck broods and dabbling duck broods (Fig. 19). Seemingly, diving duck broods show a direct relation between densities and increasing wetland size, but for both diving ducks and dabbling ducks, the density of broods dropped off sharply for wetlands >10 ha in size.

Dabbling duck broods generally used wetlands of all sizes. Exceptions were wetlands ≤0.04 ha, where broods of northern shovelers and blue-winged teal only were seen (Table 37). In contrast, with the exception of ruddy ducks, diving duck broods seldom used wetlands <0.4 ha in size.

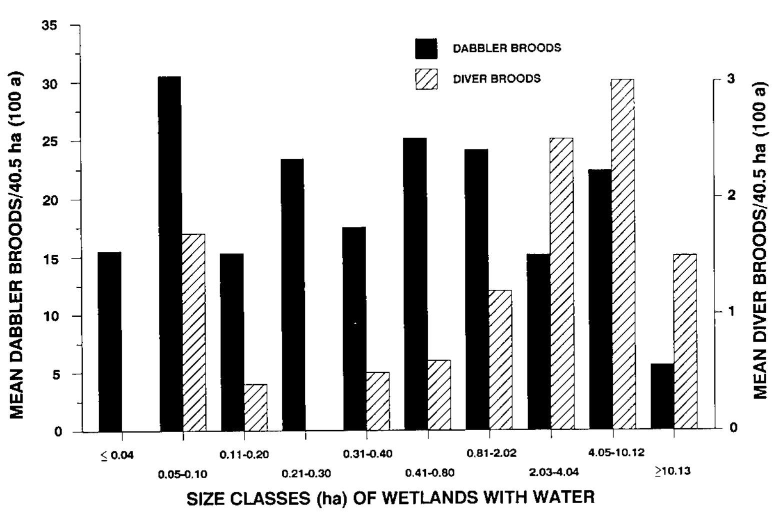

Fig. 19. Comparison of mean brood densities of dabbling and diving ducks by size classes of wetlands with water, Woodworth Study Area, 1965–81.

Table 37. *Brood densities of 12 duck species, expressed as broods per 40.5 ha, by wetland size class during July and August, Woodworth Study Area, 1965–75.*

Species	Broods per 40.5 ha in wetlands of size class									
	≤0.9	0.10–0.25	0.26–0.50	0.51–0.75	0.76–1.00	1.01–2.00	2.01–5.00	5.01–10.00	10.01–25.00	≥25.01
Dabbling ducks										
Mallard	0.0	0.9	0.4	1.9	0.5	1.4	1.5	1.9	2.1	0.6
Gadwall	0.0	1.7	0.8	0.5	1.0	1.4	1.1	0.9	4.3	1.5
Northern pintail	0.0	2.6	0.4	0.9	1.0	0.1	0.5	0.3	1.0	0.5
Green-winged teal	0.0	0.9	0.4	0.5	1.0	0.3	1.4	0.3	0.3	0.1
Blue-winged teal	11.0	22.6	13.4	17.9	12.0	20.5	17.8	10.1	12.7	2.6
Northern shoveler	5.5	0.9	0.0	2.4	2.0	1.3	1.6	0.9	1.1	0.2
American wigeon	0.0	0.9	0.0	0.0	0.0	0.1	0.3	0.6	1.0	0.1
Total dabbling ducks	16.5	30.4	15.4	24.0	17.5	25.2	24.3	15.2	22.4	5.6
Diving ducks										
Redhead	0.0	0.0	0.0	0.0	0.0	0.1	0.1	1.3	0.6	0.3
Canvasback	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.6	0.1
Lesser scaup	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.5	0.5
Ring-necked duck	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1
Ruddy duck	0.0	1.7	0.4	0.0	0.5	0.4	0.8	1.3	1.3	0.5
Total diving ducks	0.0	1.7	0.4	0.0	0.5	0.6	1.2	2.5	3.0	1.5
Grand total	16.5	32.2	15.8	24.0	18.0	25.8	25.5	17.7	25.4	7.1

During the 11-year sampling period, no broods were counted on Class I, II^{t}, T-2, T-3, or T-4 wetlands and, with the exception of blue-winged teal, no other broods were counted on Class I^{t} or II wetlands (Table 38). Class III and IV wetlands and wetlands with dams were generally used by all species of broods similar to their occurrence in the total brood population. Class III^{t} wetlands were used by broods of dabbling but not diving ducks, and only mallard broods were counted on wetland dugouts. Class V wetlands were generally used by all species of duck broods but were not used in proportion to their availability. Class V wetlands were approximately 20 ha in size.

Brood-to-wetland Relations and Brood Sizes

There was a significant relation ($r^2 = 0.41$, $P < 0.01$, 16 df) between the estimated total of all species of duck broods and percent of basins with water during 1–15 May (Fig. 20). The relation between estimated numbers of broods per year and percent of basins with water during 1–15 May were also examined for each species (Table 39). As with pairs, dabbling duck broods related better with early May water ($r^2 = 0.62$) than did diving duck broods ($r^2 = 0.28$). Canvasbacks, American wigeon, and lesser scaup showed a negative relation to May water counts; whereas, northern pintails, blue-winged teal, northern shovelers, and ruddy ducks showed a positive relation.

Average brood sizes were based on 1,425 sightings during July and August censuses over 17 years (Table 40). These data include only those sightings where all ducklings were believed seen. Overall, we found the August brood counts yielded about the same number of broods as the July counts. Mean brood size ranged from 7.5 for lesser scaup to 4.4 for northern pintails and averaged 6.4 for all species. Dabbling duck broods averaged one duckling per brood larger than diving ducks (6.6 vs. 5.6). This difference was largely accounted for by the smaller clutch and brood sizes of ruddy ducks.

Without attrition or with a constant brood survival, mean brood sizes would increase in number relative to increasing age of broods because early clutches are generally larger than later clutches. For July and August counts combined, mean brood size generally declined from Class I (6.7) to Class III (5.6) ducklings when all species were grouped. This change suggested duckling attrition occurred within broods. Small samples prevented a more intensive analysis among the independent age classes among species. However, when broods were grouped by three major age classes (I, II, III) and July and August counts were combined, brood sizes averaged consistently higher for July counts than for August counts. These data demonstrate an important bias (Cowardin and Johnson 1979; M. C. Hammond, Northern Prairie Wildlife Research Center, unpublished report) in reported brood sizes if broods are not sampled throughout the nesting and brood-rearing seasons. This bias can be further confounded by differential nesting chronology among species. For example, samples of Class III broods existed for only 3 of 12 species in July counts and 10 of 12 species in August counts; 3 of 12 species were not represented among Class II broods in July counts.

Declines in Duck Production

The number of ducklings to reach flight age also was affected by the decrease in average clutch size between early- and late-laid clutches (11.0 vs. 7.8; Fig. 17), which again was reflected by the decrease in average brood size between July and August counts (7.2 vs. 5.7; Table 40). This subtle and often unnoticed decline in clutch sizes during renesting efforts throughout the nesting season was indirectly caused by high rates of predation of early clutches. Unlike other types of production loss, management strategies can be employed to reduce this loss; specifically, habitats can be managed to reduce predator effectiveness; predator numbers or access to nests can be reduced to achieve higher rates of success for early clutches. Our data suggest that average annual recruitment can be enhanced by about 30% (Table 41) if early nesting attempts are successful as compared to later, renesting efforts. Obviously, any attempt to effectively manage for greater nest success will necessitate some means of reduction in overall nest predation or destruction.

Estimates of Duck Loss

We were able to assess duckling attrition between nesting and fledging periods with our methods of counting pairs and broods and evaluating nest success. Because of the apparent bias between mean brood sizes during early July and late August

Table 38. *Brood densities of 12 duck species, expressed as broods per 40.5 ha, by wetland class during July and August, Woodworth Study Area, 1965–75.*

Species	Broods per 40.5 ha by size class[a] of wetlands										
	I	I[t]	II	II[t]	III	III[t]	T-2+3+4	IV	V	Dams	Dugouts
Dabbling ducks											
Mallard	0.0	0.0	0.0	0.0	1.3	0.0	0.0	1.5	0.3	2.0	9.1
Gadwall	0.0	0.0	0.0	0.0	1.5	5.0	0.0	2.6	0.1	4.3	0.0
Northern pintail	0.0	0.0	0.0	0.0	0.7	5.0	0.0	0.6	0.6	0.9	0.0
Green-winged teal	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.4	0.0	0.2	0.0
Blue-winged teal	0.0	73.0	2.4	0.0	14.2	0.0	0.0	11.0	0.4	11.2	0.0
Northern shoveler	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.8	0.0	1.0	0.0
American wigeon	0.0	0.0	0.0	0.0	0.5	5.0	0.0	0.4	0.0	0.2	0.0
Total dabbling ducks	0.0	73.0	2.4	0.0	20.5	15.0	0.0	17.3	1.4	19.8	9.1
Diving ducks											
Redhead	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.5	0.4	0.2	0.0
Canvasback	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.4	0.0	0.1	0.0
Lesser scaup	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6	1.0	0.0
Ring-necked duck	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0
Ruddy duck	0.0	0.0	0.0	0.0	0.3	0.0	0.0	1.2	0.5	0.8	0.0
Total diving ducks	0.0	0.0	0.0	0.0	0.5	0.0	0.0	2.4	1.6	2.2	0.0
Grand total	0.0	73.0	2.4	0.0	21.0	15.0	0.0	19.7	3.0	22.0	9.1

[a] Size classes according to classification of Stewart and Kantrud 1971.
[t] Superscript t indicates tillaged class.

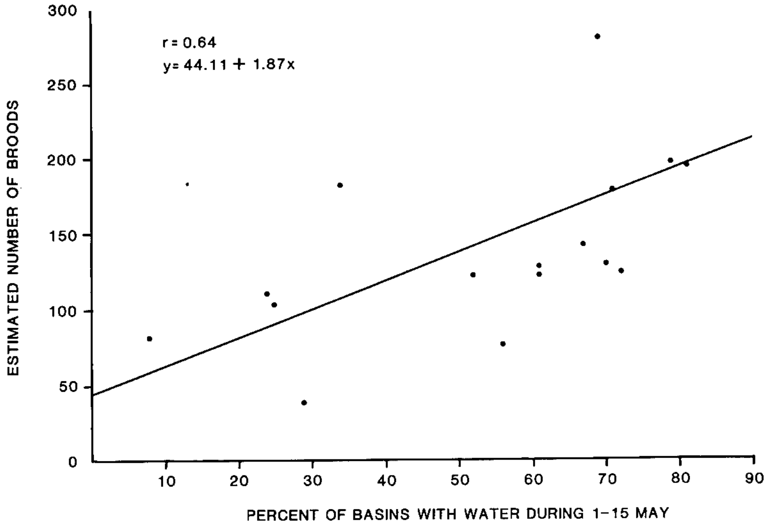

Fig. 20. Broods of all duck species in relation to percent of 548 basins with water during 1–15 May, Woodworth Study Area, 1965–81.

brood counts (Table 40), duckling loss was estimated as the difference between average clutch sizes and average brood sizes for July and August counts combined. Duckling loss between the mean clutch size and average brood size ranged from 44% for northern pintails to 23% for American wigeon and averaged 29% for all species (Table 41).

An average 24% of the duckling mortality (2.6 young per brood) was estimated to occur between hatching and age Class Ib, whereas only 4% (0.4 young per brood) occurred between age Class Ib and the average total brood size. Thus, approximately 85% of duckling mortality, an average loss of 2.2 ducklings per brood, occurred between hatching and age Class Ib, or approximately 2 weeks of age, and 15% between Class Ib and mean brood size. This agrees with Ball et al. (1975), Reed (1975), Cowardin and Johnson (1979), Talent et al. (1983), and Duebbert and Frank (1984). The latter reported a difference of about 2.5 ducklings between average clutch size of nests and average Class I brood size. Talent et al. (1983) found that 85% of the mortality, of 13 mallard broods in which all young were lost, occurred within the first 2 weeks after hatching and 52% mortality for entire broods during a 2-year study. Ball et al. (1975) found that most total brood loss by mallards also occurred during the first 2 weeks after hatching in Minnesota. Cowardin et al. (1985) reported that 26% of radio-marked mallard hens lost broods between hatching and fledging. Our data also indicated that similar duckling loss occurred among all species, except possibly northern pintails for which we had only a small sample of brood observations.

Duckling loss between Class I and III broods averaged 16%, or 1.1 young per brood, during the 17-year study (Table 42). Attrition estimates in Table 43 do not include losses of entire broods

Table 39. *Linear regression values between broods per year and percent of wet basins during 1–15 May duck counts, Woodworth Study Area, 1965–81.*

Species	r-values [a]
Dabbling ducks	
Mallard	0.0363
Gadwall	0.1197
Northern pintail	0.5066
Green-winged teal	0.4720
Blue-winged teal	0.7035
Northern shoveler	0.6823
American wigeon	−0.0374
Total dabbling ducks	0.6226
Diving ducks	
Redhead	0.0631
Canvasback	−0.0548
Lesser scaup	−0.1654
Ruddy duck	0.5048
Ring-necked duck	0.2851
Total diving ducks	0.2814
Total broods	0.6417

[a] r-values >0.48 were significant, 16 df.

Table 40. *Mean cumulative brood size of 12 duck species by age class and month, Woodworth Study Area, 1965–81.*[a]

Species	Class I			Class II			Class III			17-year mean, all classes		
	July	August	July and August	July	August	July and August	July	August	July and August	July	August	July and August
Dabbling ducks												
Mallard	6.3	6.1	6.2	5.4	5.5	5.5	—[b]	5.7	5.7	5.9	5.7	5.8
Gadwall	8.1	6.4	7.3	7.8	6.9	7.0	—	—	—	8.0	6.6	7.2
American wigeon	7.9	5.0	7.3	—	5.6	5.6	—	6.0	6.0	7.9	5.5	6.6
Green-winged teal	7.0	4.8	5.5	—	6.3	6.3	—	4.0	4.0	7.0	5.1	5.4
Blue-winged teal	7.5	5.2	6.9	7.7	5.6	6.7	6.5	5.8	5.9	7.6	5.6	6.7
Northern shoveler	6.7	4.4	5.8	6.3	5.3	5.7	7.5	4.4	5.0	6.6	4.9	5.6
Northern pintail	9.3	3.0	6.6	4.3	3.3	3.9	1.0	4.5	3.8	5.3	3.6	4.4
Total dabbling ducks	7.6	5.8	6.9	7.3	5.8	6.5	6.3	5.6	5.7	7.4	5.8	6.6
Diving ducks												
Redhead	7.7	6.0	6.6	6.7	5.2	5.6	—	3.7	3.7	7.5	5.6	6.2
Canvasback	5.5	5.0	5.4	4.8	4.7	4.7	—	3.4	3.4	5.0	4.5	4.7
Lesser scaup	8.0	6.5	7.0	—	7.9	7.9	—	—	—	8.0	7.4	7.5
Ring-necked—duck	8.0	4.0	6.0	10.0	5.5	7.0	—	8.0	8.0	9.0	5.8	6.8
Ruddy duck	4.9	5.2	5.1	6.8	3.7	4.0	—	5.7	5.7	5.2	4.5	4.7
Total diving ducks	6.2	5.7	5.9	5.4	5.5	5.5	—	4.4	4.4	5.9	5.5	5.6
Total broods	7.4	5.7	6.7	7.1	5.8	6.3	6.3	5.5	5.6	7.2	5.7	6.4

[a] Only broods with complete counts.
[b] Indicates no data.

Table 41. *Reduction of brood size of 12 duck species between age classes, Woodworth Study Area, 1965–81.*

Species	Average successful clutch size	17-year average brood size	Brood size reduction between average successful clutch size and average total brood size		Brood size reduction between average successful clutch size and average Class I[b] brood size		Brood size reduction between average size Class I[b] brood and average total brood size	
			Number	Percent	Number	Percent	Number	Percent
Dabbling ducks								
Mallard	9.2	5.8	3.4	37	2.3	25	1.1	16
Gadwall	9.7	7.2	2.5	26	1.9	20	0.6	8
American wigeon	8.6	6.6	2.0	23	1.8	21	0.2	3
Green-winged teal	8.8	5.4	3.4	39	2.8	32	0.6	10
Blue-winged teal	10.2	6.7	3.5	34	3.4	33	0.1	1
Northern shoveler	9.9	5.6	4.3	43	3.5	35	0.8	13
Northern pintail	7.8	4.4	3.4	44	0.3	4	3.1	41
Total dabbling ducks	9.8	6.6	3.2	33	2.7	28	0.5	7
Diving ducks								
Redhead	10.0[a]	6.2	3.8	38	3.3	33	0.5	7
Canvasback	7.7[a]	4.7	3.0	39	2.3	30	0.7	13
Lesser scaup	9.9	7.5	2.4	24	3.1	31	1.3[d]	19[d]
Ring-necked duck	9.2[b]	6.8	2.4	26	5.2	57	2.8[d]	70[d]
Ruddy duck	6.6[a]	4.7	1.9	29	1.9	29	0.0	0
Total diving ducks	8.7[c]	5.6	3.1	36	3.1	36	0.0	0
Total broods	9.0[c]	6.4	2.6	29	2.2	24	0.4	4

[a] Based on data by Stoudt (1971).
[b] Based on data by Smith (1971).
[c] Mean of means for species in these groups.
[d] These were increases in brood sizes and not attrition.

Table 42. *Reduction of brood size of 12 duck species between age classes for July and August counts, Woodworth Study Area, 1965–81.*

Species	Reduction of brood size from average age Class I to Class III ducklings: Number	Percent
Dabbling duck		
Mallard	0.5	8
Gadwall	0.3[a]	4[a]
American wigeon	1.3	18
Green-winged teal	1.5	27
Blue-winged teal	1.0	14
Northern shoveler	0.8	14
Northern pintail	2.8	42
Total dabbling ducks	1.2	17
Diving duck		
Redhead	2.9	44
Canvasback	2.0	37
Lesser scaup	0.9[b]	13[b]
Ring-necked duck	2.0[b]	33[b]
Ruddy duck	0.6[b]	12[b]
Total diving ducks	1.5	25
All broods	1.1	16

[a] Based on Class II brood size because of no sample of Class III broods.

[b] Average brood size increased between Classes I and II; no sample of Class III broods.

between hatching and counting, thereby biasing these duckling loss rates downward.

We did not specifically attempt to assess duckling mortality between their nest and first pond visited; however, instances of Class Ia duckling deaths were known to have occurred on the study area or nearby. We think the amount of duckling loss between the nest and first pond visit, usually during the first 24 h after hatching, is probably small, relative to the overall duckling mortality that occurs between hatching and fledging. Furthermore, even if there was large loss, it would be extremely difficult to apply any practical management strategy, except possibly intensive predator control, to ameliorate this duckling mortality.

Duckling loss between hatching and fledging is hard to assess and, in our opinion, is one of the greater problems of waterfowl management in need of immediate research. At present, not enough information exists to tell managers what proportions of duckling loss are due to habitat conditions, disease, weather, predation, or starvation.

Hen Success and Recruitment

A hen was termed successful when at least one duckling was fledged from one or more nesting attempts. We used the brood to pair ratio as a measure of hen success and assumed that brood ingress and egress were equal, and that all broods and pairs were seen. During the 17 years, an average of 30% of the hens were successful in hatching a clutch, getting the ducklings to water and having them survive long enough to be counted (Table 43). Our estimate of 30% average hen success agrees with the estimates of 32% hen success from long-term studies in southern Canada (Smith 1971; Stoudt 1971). At Woodworth, only 7 of the 17 years had hen success >30% and there were only two instances (1966–67, 1976–77) of consecutive years with hen success >30%. Among the 12 duck species at the WSA, green-winged teal, blue-winged teal, American wigeon, canvasbacks, ring-necked ducks, and ruddy ducks had hen success estimates averaging >30%. The poorest year for hen success was 1973 (15%) and the best was 1971 (64%).

The brood to pair ratio is only an index to success of the nesting population. Mortality among hens during the nesting and brood-rearing seasons, and total loss of broods before they are counted, are factors that strongly affect hen success estimates. Although we did not attempt to assess adult duck mortality, a concurrent study in the same region estimated an average annual loss of 13.5% of hens and 4.5% of drakes to red foxes (Sargeant et al. 1984). Furthermore, the capability of observers to count and separate the nesting population from migrants and to observe all broods are also factors that affect estimates of hen success.

Cowardin and Johnson (1979) estimated mallard hen success (H) from an estimate of nest success rates (P) using the formula $H = Pe^{(1-P)}$. Application of their formula to our nest success rates ($P = 0.16$) yielded a hen success estimate of 32%, which agrees with our hen success estimate of 30% based on brood to pair ratios.

Recruitment rates were estimated from direct counts of the breeding population, number of broods produced, and brood size. Our estimates of

average recruitment included 0.93 for ring-necked ducks down to 0.40 for ruddy ducks and averaged 0.59 for 12 species (Table 44). Cowardin et al. (1985) indicated that mallard populations in North Dakota would remain stable with a nest success rate of 15.2%, a hen success rate of 0.31, and a recruitment rate (R) of 0.53; where $R = H_z B/2$ (Cowardin and Johnson 1979). The mallard recruitment rate at the WSA averaged 0.50, suggesting a nearly stable to slowly declining population. The recruitment rate for mallards at the WSA was about midway between the highest and lowest estimated rates for the 12 species of ducks nesting on the area.

The number of fledged ducklings produced per year averaged 579 (Table 44), from an average duck population of 492 pairs, approximately 1.18 fledglings per pair per year.

Conclusions

Generally, the methods used to count or evaluate wetlands, ducks, and vegetation structure were adequate for the study. However, some methods such as the nest surveys and the pair and brood counts required considerable amounts of time and labor to conduct. Of all the kinds of data collected, the brood counts were probably the most unreliable because broods are hard to see in vegetated wetlands; if complete brood count data were possible, it would be the most valuable of the data sets.

Our pond occupancy data demonstrates considerable variability among the seasonal time of surveys and the number of wet basins present. Thus, we believe pond occupancy data are poor indexes of specific selection behavior by ducks for various wetland characteristics unless the data are collected in a strictly coordinated effort over time and area.

We found the 1–15 May count usually yielded the best pair population estimates for mallards, northern pintails, canvasbacks, and green-winged teal, and the 20 May–7 June count for all other species. Occasionally, the first count also was used in pair estimates for blue-winged teal. Our recommended census periods approximate those of Dzubin (1969), Smith (1971), and Stoudt (1971).

Annual federal hunting regulations are based, in part, on a single production estimate from data collected in July during aerial brood surveys (Henry et al. 1972). This corresponds to dates when several states, including North Dakota (Schroeder 1971), and several Canadian provinces conduct roadside brood surveys. Based on our hatching chronology data (Table 16), an average of 43% of the potential broods would not have been counted if surveys were made on 10 July, 33% on 15 July, 22% on 20 July, and 15% on 25 July. Similarly, an average of only 50% of duck broods was counted during our July censuses, which approximated the timing of the Service's annual July production surveys. Our study showed that when only one brood survey is made, it should be later in the nesting season, preferably between 25 July and 10 August. However, such a survey would be too late for the present waterfowl regulations-setting schedule.

Ducks nested in all available life-forms and communities of vegetation on the study area and most plant species were associated with duck nests at one time or another during the study. However, wolfberry (*Symphoricarpus occidentalis*), in our opinion, was the species most important to duck nesting in native prairie habitats whereas alfalfa (*Medicago sativa*) was the most important forb in planted grasslands.

Predation was a key factor limiting waterfowl reproductive success during the study. Results showed that the effects of predation could be abated by establishing and maintaining good stands of suitable nesting cover and with no major effort to control predator populations during some years. However, management of upland habitats on our large study area only kept the annual nesting populations of waterfowl producing at an average nest success rate slightly above the threshold believed necessary to sustain or increase a population. This was accomplished despite human disturbances necessary to conduct field research; thus, even higher waterfowl production would be expected with good habitat management in the absence of research activities such as occurred on the Woodworth Study Area. However, to increase populations substantially, control of predators or predator access would enhance production even more, especially in combination with good habitat management as demonstrated by Duebbert (1969) and Duebbert and Kantrud (1974).

The greatest loss of ducklings was apparent in the first 2 weeks following hatching. Future re-

Table 43. *Estimates of broods per 100 pairs of ducks, Woodworth Study Area, 1965–81.*[a]

Species	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	Mean
Mallard	18	50	17	3	62	19	57	17	7	30	31	4	54	23	20	16	50	25
Gadwall	29	45	25	24	64	15	73	19	8	54	16	19	61	22	21	33	28	30
Northern pintail	38	41	15	36	79	11	8	11	9	34	14	7	20	7	24	6	15	22
Green-winged teal	33	90	54	57	33	25	64	8	7	75	33	0	0	25	0	10	0	32
Blue-winged teal	30	70	36	31	65	28	79	34	29	21	38	4	31	19	23	21	26	33
Northern shoveler	23	70	45	19	61	23	27	31	13	25	18	3	14	15	11	14	6	25
American wigeon	31	42	7	22	44	20	100	24	0	36	14	0	33	33	83	23	88	31
Redhead	50	11	40	21	19	44	33	29	0	32	11	18	0	6	5	44	23	21
Canvasback	9	67	0	0	50	50	0	100	50	250	22	133	0	33	79	28	93	50
Lesser scaup	26	21	0	23	32	14	41	17	0	3	9	13	0	31	0	26	52	18
Ruddy duck	23	127	250	22	36	500	200	38	0	26	33	313	0	29	4	33	13	39
Ring-necked duck	0	40	50	0	200	0	0	0	0	0	0	100	0	0	0	50	0	32
Total	28	58	34	25	60	23	64	27	15	29	29	61	36	22	30	22	33	30

[a] Numbers greater than 100 are due to the difficulty of determining accurate pair estimates or brood immigration into the area or both.

Table 44. *Average production and recruitment rates of young for 12 duck species, Woodworth Study Area, 1965–81.*

Species	Average pair population (PP)	Hen success rate (H)	Average brood size at fledging (B)[a]	Recruitment rate (R)[b]	Average young produced per year[c]
Mallard	53	0.25	5.7	0.49	53
Gadwall	68	0.30	7.3	0.76	104
Northern pintail	31	0.22	3.8	0.29	18
Green-winged teal	9	0.32	4.0	0.44	8
Blue-winged teal	225	0.33	5.9	0.68	307
Northern shoveler	29	0.25	5.0	0.43	25
American wigeon	11	0.31	6.0	0.69	15
Redhead	18	0.21	3.7	0.27	10
Canvasback	6	0.50	3.4	0.59	7
Lesser scaup	23	0.18	7.5	0.47	22
Ring-necked duck	1	0.39	6.8	0.92	2
Ruddy duck	20	0.32	3.6	0.40	16
Total	492	0.30	5.6	0.58	579

[a] Average brood size at Class III brood size was used, or the nearest estimate, and it was assumed that very little duckling loss occurred between Class III brood size and fledging.

[b] $R = HZB/2$ where $Z = 0.70$ for survival of broods from hatch time to census periods (Cowardin and Johnson 1979).

[c] Average young produced per year = $2 \times R \times PP$

search on duckling survival should be emphasized for this age period for all species of ducks.

Our results indicate that several species of waterfowl on the 4-km^2 WSA maintained, but did not increase, their populations under the multiple kinds of land use management, despite current rates of predation and habitat degradation.

Average annual recruitment of ducks can be best enhanced if habitat and predator management strategies focus on successful production from the first (earliest) nesting attempts and on survival of ducklings through their first 2 weeks of life after hatching. Our assessment of waterfowl recruitment would have been enhanced by banding and marking a sample of ducklings and adults annually.

We support Boyd (1973): "If natural resource (waterfowl) management is to be effective in the long-term, it must be based on the identification and understanding of dynamic processes acting over large areas and long periods of time—decades and centuries, rather than days and years." The slowly changing prairie and parkland environment over thousands of years makes even 15-, 20-, and 25-year waterfowl studies seem relatively short-term. Long-term studies usually receive low priority in any administrative system, wherein dollars and labor-hours are limited. Often, it seems apparent that the progression of waterfowl management and research is measured more by the number of job completion reports and publications rather than by our actual accomplishments towards production and solution, no matter how long it may take.

Recommendations

We recommend that long-term waterfowl studies be continued at the Woodworth Study Area and additional locations within broad ecological habitat associations in the glaciated prairie pothole region. Most waterfowl ecology field studies have been relatively short-term because of graduate school tenure, funding allocations, and employee transfer. Even when graduate studies are sequential (e.g., three consecutive 2-year master's programs), their total is still relatively short-term.

If future long-term studies are to be conducted on the WSA or some similar large tract of land, we would also recommend using aerial photography and remote-sensed data to evaluate land use changes, vegetation changes, and wet–dry conditions of wetlands. Use of these procedures would greatly enhance data accuracy and would provide better permanent records of the overall terrestrial aspects for any future study.

Upland-nesting waterfowl were emphasized during this study; in future studies we would recommend more emphasis on over-water nesting waterfowl and shorebirds. We would also recommend a more integrated study approach with special emphasis on predator effects and behavior and on buffer-prey species abundance, particularly of small mammals, passerines, amphibians, and insects. The May breeding pair surveys have usually been concerned only with numbers of wet ponds to describe spring water conditions (U.S. Fish and Wildlife Service 1976). At the WSA between 5 and 10% of the basins did not hold water long enough to be of any substantive value to ducks. Since all (100%) of the basins cannot hold water until the 1–15 May counts, numerically what then constitutes a wet year for ducks, and is it predictable? We arbitrarily referred to a wet year as one in which at least 65% of the basins were full or nearly full to capacity during 1–15 May. There is a strong distinction between basin fullness as compared to just wetness (i.e., numbers of wet ponds regardless of the amount of fullness). We recommend that all agencies making production estimates from pair and brood counts and wet pond counts look deeper at what constitutes a wet pond and its suitability for waterfowl use.

To get reasonable estimates of the nesting population, we recommend a minimum of two pair counts: a first census during the first 2 weeks in May and a second census during the last week of May or the first 2 weeks in June. If possible, the first count should closely coincide with the onset of blue-winged teal nesting and the second with the start of gadwall nesting.

If breeding pairs are to be estimated from one census only, we recommend a count during 20 May–7 June. Occasionally, we noted an influx of mallards during early June; possibly these were pairs that displaced from the intensively-farmed and drained drift prairie area of eastern North Dakota when early nesting attempts were destroyed. The influx of mallards during early June would have less effect on the overall breeding pair estimates if only one count was made during 20 May–7 June, compared to an earlier period

when there would be greater numbers of lesser scaup, redheads, and ruddy ducks, many of which would be migrants.

Research is needed on the criteria of what constitutes a blue-winged teal pair. We suspect one female may often be represented by more than one male during the same count; thus, some lone drakes may be bachelor males. At present, each lone drake is representative of a nesting hen in groups of up to five (Hammond 1969).

Compared to Service aerial surveys data, we seldom, if ever, had densities of American wigeon or green-winged teal greater than 3.2 pairs per square kilometer (2 pairs per square mile); however, the current index adjustment factor for May surveys of ducks increases wigeon numbers by 15 times. We recommend a study to compare present ground and aerial techniques used by various agencies to estimate waterfowl recruitment on the same area.

Research needs to consider a greater species variety of plants to be used in seeding nesting cover. Our study, like many others, dealt primarily with mixtures of tame grasses and legumes. More emphasis should be placed on native grass plantings, on plantings of nesting cover composed of aromatics and armed (thorny, prickly, sawtoothed leaved) vegetation, and on various patterns of cover for greater edge and cover diversity. We believe that predator effectiveness might be reduced further by using some of these new cover types.

For lands that have been tilled in the past, we recommend planting nesting cover that is tall. In our study, plantings with a mixture of cool-season grasses and legumes have this characteristic and were rather productive for most upland nesting waterfowl. For lands with native prairie cover, we recommend against the use of annual haying, grazing, or burning, but we encourage periodic manipulations with 1–3-years of rest between treatments for all cover types. We advise a status quo of management operations during and 1 year following all years with extreme wet or dry weather effects, unless there are sound reasons for such decisions. We also recommend that most land-use practices be conducted before 15 April or after 25 July to be least detrimental to nest success.

In this area of the glaciated prairie pothole region, we recommend against starting land-use treatments on duck production lands before 25 July in average or above average precipitation years, and no sooner than 15 July, even in drought years. We also concur with Duebbert and Frank (1984) that 1 August would be the preferable date for initiating mowing on areas managed primarily for production of ground-nesting ducks and winter cover for other wildlife. Further, in many instances, 1 August would also be a preferable initiation date for burning and grazing treatments on native mixed-grass prairie, if the objective is to favor cool-season native plants.

Grazing, burning, haying, and mowing are tools used for managing upland habitats. The timing of these treatments is critical in relation to the potential duck hatch. An appropriate overall land management strategy is to treat only a portion of a management unit because the total land base should not be treated during any one year. However, during drought or other emergency situations, public agencies are often requested to enlarge the amount of land base treated by grazing or haying to satisfy demands of private farmers and ranchers. We suggest that grazing, burning, haying, and mowing treatments be applied periodically, in as short of time as possible, and either before or after the nesting season.

Our native prairie habitat research was limited to season-long grazing and to mostly spring burning management. We support expanding of the research to include additional types of specialized grazing systems and to fall burning efforts, both of which show initial promise for increasing waterfowl production for private as well as public lands, and in wetlands as well as uplands.

Generally, nest success averaged greater in larger sized fields. We suggest, where possible, management of fields >8 ha in size would be more beneficial to duck production than fields <8 ha in size, regardless of the upland habitat type. Nelson and Duebbert (1974) and Stoudt (1969) also suggested that nest success was greater in larger fields of cover than in smaller areas.

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Appendix A. Precipitation data (cm), Woodworth, North Dakota, 1962–81

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
1962[a]	1.35	0.58	3.98	1.48	15.67	6.38	26.55	7.03	8.40	0.58	1.88	0.15	74.00
1963[a]	0.28	0.33	0.73	4.55	5.03	6.15	8.25	7.43	2.53	0.63	0.00	2.05	38.00
1964[a]	0.58	0.38	1.15	6.48	6.95	15.70	7.55	7.83	3.38	0.53	1.00	2.10	53.60
1965[a]	0.83	0.28	1.70	4.85	6.55	5.78	6.50	18.55	8.10	1.88	1.75	0.55	57.30
1966	0.00	0.28	2.18	3.85	1.88	10.60	5.85	4.18	1.68	3.48	0.20	0.40	34.55
1967	0.50	0.33	0.55	2.88	2.38	4.03	0.85	2.03	3.88	4.68	0.00	0.98	23.05
1968	0.00	0.00	2.48	6.83	7.38	11.38	1.35	8.60	4.03	0.98	0.00	0.83	43.83
1969	1.68	0.78	0.95	1.60	7.38	9.83	3.68	1.93	1.98	1.43	0.00	1.03	32.23
1970	0.30	0.48	0.48	4.20	3.43	10.28	5.48	1.08	3.10	2.18	1.70	0.48	33.15
1971	1.00	0.30	0.38	2.93	5.40	14.13	4.70	2.23	4.18	8.30	0.15	0.38	44.05
1972	0.65	0.53	0.75	2.43	5.18	4.38	6.38	4.70	2.00	3.03	0.20	0.88	31.08
1973	0.20	0.13	3.40	2.33	1.80	6.45	2.13	4.39	14.35	4.48	0.83	0.65	41.03
1974	0.28	0.15	1.03	5.65	9.83	3.10	6.45	5.93	0.35	1.83	2.38	0.28	37.23
1975	1.00	0.15	0.88	5.85	4.55	21.43	3.28	6.80	3.75	1.00	0.43	0.65	49.27
1976	0.95	0.45	0.78	5.93	1.80	6.68	1.70	1.63	0.48	0.03[b]	0.28	0.28	20.93
1977	0.98	0.40	1.23	1.35	8.23	5.00	12.63	4.90	12.95	2.03	2.75	1.08	53.50
1978	0.03	0.00	0.05	2.65	7.70	10.05	4.78	3.13	4.03	0.88	1.73	0.53	35.53
1979	0.56	1.25	1.53	3.18	3.95	11.68	8.93	4.58	1.33	0.80	0.23	1.03	38.93
1980	0.66	0.43	0.53	0.00	3.63	10.65	4.55	4.43	5.30	6.10	0.63	0.43	44.00
1981	0.35	0.78	0.83	3.48	3.38	8.75	6.98	2.68	5.30	3.40	1.20	0.70	37.80
Total	9.60	8.03	25.59	72.50	112.10	182.43	128.57	103.97	91.10	48.25	17.34	15.46	823.06
$\bar{x}$ (n=20)	0.48	0.40	1.28	3.63	5.61	9.13	6.43	5.20	4.55	2.40	0.88	0.78	41.18
Min–max	0.00–1.68	0.00–1.25	0.05–3.98	0.00–6.83	1.80–15.67	3.10–21.43	0.85–26.55	1.08–18.55	0.35–14.35	0.03–8.30	0.00–2.75	0.15–2.10	20.93–74.00

[a] Readings taken in Woodworth; other readings taken 4.8 km east of Woodworth.
[b] Records indicate traces.

Appendix B. Bird species observed, Woodworth Study Area, 1963–81

Common name	Scientific name
Western grebe	*Aechmophorus occidentalis*
Horned grebe	*Podiceps auritus*
Red-necked grebe	*Podiceps grisegena*
Eared grebe	*Podiceps nigricollis*
Pied-billed grebe	*Podilymbus podiceps*
American white pelican	*Pelecanus erythrorhynchos*
Double-crested cormorant	*Phalacrocorax auritus*
Great blue heron	*Ardea herodias*
American bittern	*Botaurus lentiginosus*
Black-crowned night-heron	*Nycticorax nycticorax*
Wood duck	*Aix sponsa*
Northern pintail	*Anas acuta*
American wigeon	*Anas americana*
Northern shoveler	*Anas clypeata*
Green-winged teal	*Anas crecca*
Cinnamon teal	*Anas cyanoptera*
Blue-winged teal	*Anas discors*
Mallard	*Anas platyrhynchos*
American black duck	*Anas rubripes*
Gadwall	*Anas strepera*
Greater white-fronted goose	*Anser albifrons*
Lesser scaup	*Aythya affinis*
Redhead	*Aythya americana*
Ring-necked duck	*Aythya collaris*
Greater scaup	*Aythya marila*
Canvasback	*Aythya valisineria*
Canada goose	*Branta canadensis*
Bufflehead	*Bucephala albeola*
Common goldeneye	*Bucephala clangula*
Snow goose	*Chen caerulescens*
Tundra swan	*Cygnus columbianus*
Hooded merganser	*Lophodytes cucullatus*
Common merganser	*Mergus merganser*
Ruddy duck	*Oxyura jamaicensis*
Red-tailed hawk	*Buteo jamaicensis*
Ferruginous hawk	*Buteo regalis*
Swainson's hawk	*Buteo swainsoni*
Northern harrier	*Circus cyaneus*
American kestrel	*Falco sparverius*
Gray partridge	*Perdix perdix*
Ring-necked pheasant	*Phasianus colchicus*

Sharp-tailed grouse	*Tympanuchus phasianellus*
American coot	*Fulica americana*
Sora	*Porzana carolina*
Virginia rail	*Rallus limicola*
Sandhill crane	*Grus canadensis*
Killdeer	*Charadrius vociferus*
American avocet	*Recurvirostra americana*
Spotted sandpiper	*Actitis macularia*
Upland sandpiper	*Bartramia longicauda*
Willet	*Catoptrophorus semipalmatus*
Common snipe	*Gallinago gallinago*
Marbled godwit	*Limosa fedoa*
Wilson's phalarope	*Phalaropus tricolor*
Black tern	*Chlidonias niger*
Rock dove	*Columba livia*
Mourning dove	*Zenaida macroura*
Black-billed cuckoo	*Coccyzus erythropthalmus*
Short-eared owl	*Asio flammeus*
Long-eared owl	*Asio otus*
Burrowing owl	*Athene cunicularia*
Great horned owl	*Bubo virginianus*
Common nighthawk	*Chordeiles minor*
Chimney swift	*Chaetura pelagica*
Northern flicker	*Colaptes auratus*
Downy woodpecker	*Picoides pubescens*
Hairy woodpecker	*Picoides villosus*
Least flycatcher	*Empidonax minimus*
Willow flycatcher	*Empidonax traillii*
Eastern kingbird	*Tyrannus tyrannus*
Western kingbird	*Tyrannus verticalis*
Horned lark	*Eremophila alpestris*
Cliff swallow	*Hirundo pyrrhonota*
Barn swallow	*Hirundo rustica*
Purple martin	*Progne subis*
Tree swallow	*Tachycineta bicolor*
American crow	*Corvus brachyrhynchos*
Black-capped chickadee	*Parus atricapillus*
White-breasted nuthatch	*Sitta carolinensis*
Marsh wren	*Cistothorus palustris*
Sedge wren	*Cistothorus platensis*
House wren	*Troglodytes aedon*
American robin	*Turdus migratorius*
Gray catbird	*Dumetella carolinensis*
Brown thrasher	*Toxostoma rufum*
Sprague's pipit	*Anthus spragueii*
Loggerhead shrike	*Lanius ludovicianus*
European starling	*Sturnus vulgaris*
Warbling vireo	*Vireo gilvus*
Red-eyed vireo	*Vireo olivaceus*
Yellow warbler	*Dendroica petechia*

Common yellowthroat	*Geothlypis trichas*
Rose-breasted grosbeak	*Pheucticus ludovicianus*
Dickcissel	*Spiza americana*
Baird's sparrow	*Ammodramus bairdii*
Sharp-tailed sparrow	*Ammodramus caudacutus*
Grasshopper sparrow	*Ammodramus savannarum*
Lark bunting	*Calamospiza melanocorys*
Chestnut-collared longspur	*Calcarius ornatus*
Song sparrow	*Melospiza melodia*
Savannah sparrow	*Passerculus sandwichensis*
Vesper sparrow	*Pooecetes gramineus*
Clay-colored sparrow	*Spizella pallida*
Red-winged blackbird	*Agelaius phoeniceus*
Bobolink	*Dolichonyx oryzivorus*
Brewer's blackbird	*Euphagus cyanocephalus*
Northern oriole	*Icterus galbula*
Orchard oriole	*Icterus spurius*
Brown-headed cowbird	*Molothrus ater*
Common grackle	*Quiscalus quiscula*
Western meadowlark	*Sturnella neglecta*
Yellow-headed blackbird	*Xanthocephalus xanthocephalus*
American goldfinch	*Carduelis tristis*
House sparrow	*Passer domesticus*

Appendix C. Common mammals, Woodworth Study Area, 1963–81

Common name	**Scientific name**
Northern short-tailed shrew	*Blarina brevicauda*
Arctic shrew	*Sorex arcticus*
Masked shrew	*Sorex cinereus*
Little brown bat	*Myotis lucifugus*
Coyote	*Canis latrans*
Red fox	*Vulpes vulpes*
Raccoon	*Procyon lotor*
Long-tailed weasel	*Mustela frenata*
Least weasel	*Mustela nivalis*
Mink	*Mustela vison*
Badger	*Taxidea taxus*
Striped skunk	*Mephitis mephitis*
Mule deer	*Odocoileus hemionus*
White-tailed deer	*Odocoileus virginianus*
Eastern fox squirrel	*Sciurus niger*
Franklin's ground squirrel	*Spermophilis franklinii*
Richardson's ground squirrel	*Spermophilis richardsoni*
Thirteen-lined ground squirrel	*Spermophilis tridecemlineatus*
Northern pocket gopher	*Thomomys talpoides*
Northern grasshopper mouse	*Onychomys leucogaster*
Deer mouse	*Peromyscus maniculatus*
Western harvest mouse	*Reithrodontomys megalotis*
Meadow vole	*Microtus pennsylvanicus*
Muskrat	*Ondatra zibethicus*
House mouse	*Mus musculus*
Norway rat	*Rattus norvegicus*
Meadow jumping mouse	*Zapus hudsonius*
White-tailed jackrabbit	*Lepus townsendii*
Nuttall's cottontail	*Sylvilagus nuttalli*

Appendix D. Common reptiles, amphibians, and fish, Woodworth Study Area, 1963–81

Common name	**Scientific name**
Reptiles	
Eastern painted turtle	*Chrysemys picta*
Smooth green snake	*Opheodrys vernalis*
Northern redbelly snake	*Storeria occipitomaculata*
Plains garter snake	*Thamnophis radix*
Amphibians	
Tiger salamander	*Ambystoma tigrinum*
Great plains toad	*Bufo cognatus*
Canadian toad	*Bufo hemiophrys*
Boreal chorus frog	*Pseudacris triseriata maculata*
Northern leopard frog	*Rana pipiens*
Fish	
White sucker	*Catostomus commersoni*
Northern pike	*Esox lucius*
Mimic shiner	*Notropis volucellus*
Yellow perch	*Perca flavescens*
Fathead minnow	*Pimephales promelas*
Ninespine stickleback	*Pungitius pungitius*

Appendix E. Dates of first arrivals for some waterfowl species, Woodworth study area, 1966–81

Species	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981
Canada goose	3/16	3/23	3/7	4/6	4/4	3/29	3/15	3/11	2/18	3/17	3/19	3/17	4/10	4/10	3/19	3/8
White-fronted goose[a]	3/30	4/3	3/26	4/11	4/6	3/30	3/23	3/25	4/5	—[b]	4/4	3/24	4/16	4/16	4/1	4/1
Snow goose	3/30	—	4/1	—	—	3/30	3/22	3/25	4/5	—	—	3/27	4/15	4/15	4/5	3/19
Tundra swan	4/3	4/4	4/1	4/6	—	4/7	3/23	3/27	4/7	4/21	3/30	4/7	4/12	4/16	3/31	3/30
Mallard	3/16	3/23	3/16	4/6	4/5	3/29	3/15	3/18	4/5	3/20	3/19	3/19	3/26	4/14	3/30	3/14
Northern pintail	3/16	3/23	3/16	3/27	4/6	3/29	3/15	—	4/5	3/19	3/19	3/24	3/26	4/15	3/31	3/23
Gadwall	3/30	4/2	3/29	4/11	4/7	4/7	4/10	3/21	4/11	4/28	—	3/27	3/30	4/16	4/8	3/25
Blue-winged teal	4/14	4/12	4/10	4/11	4/9	4/9	4/17	4/18	4/15	4/22	4/8	4/5	—	4/17	4/9	4/4
Green-winged teal	4/4	4/2	3/31	4/7	4/7	4/7	4/10	—	4/10	4/21	4/1	3/14	—	4/23	4/4	3/24
Northern shoveler	3/30	4/2	—	4/11	4/7	4/8	4/10	3/25	4/10	4/21	4/1	3/27	3/30	4/16	4/7	3/28
American wigeon	4/16	3/31	3/27	4/7	4/6	3/30	3/21	3/21	—	4/28	3/25	3/27	3/30	4/16	4/1	3/27
Wood duck	—	—	—	—	—	—	—	4/22	4/12	4/21	4/1	4/11	4/9	4/16	4/8	5/29
Redhead	3/30	4/2	3/27	4/11	4/7	4/7	3/22	—	4/10	4/21	3/25	3/27	3/30	4/16	4/6	3/24
Canvasback	3/30	4/2	3/30	4/11	4/7	4/7	4/7	4/1	4/10	4/21	—	3/27	—	4/17	4/5	3/27
Lesser scaup	4/13	3/26	3/27	4/11	4/7	3/31	3/24	3/21	4/10	4/17	3/30	3/27	—	4/16	4/2	3/24
Ring-necked duck	—	4/2	3/30	4/11	4/7	4/7	3/22	—	4/10	4/21	3/30	3/25	3/30	4/16	4/5	3/24
Bufflehead	4/14	—	3/31	4/11	4/7	4/7	3/22	—	4/16	4/17	—	—	—	—	4/9	3/25
Common goldeneye	3/30	4/2	3/28	—	4/6	4/9	3/22	—	4/15	4/19	3/25	3/10	3/30	4/16	3/31	3/27
Ruddy duck	4/28	—	4/22	4/18	—	5/3	4/20	5/16	4/28	4/29	4/26	4/11	3/20	4/30	4/20	4/16
Common merganser	3/30	3/25	3/29	4/6	4/7	3/29	—	—	—	4/16	3/25	3/25	—	4/16	4/7	3/23
American coot	—	4/30	3/31	4/11	4/9	4/9	—	4/11	4/16	4/22	—	4/11	—	4/17	4/2	4/2

[a] Greater.
[b] No data.

Glossary

Age when found Number of eggs plus incubation stage in days. (Assume that one egg is laid each day)

Brood A brood was indicated and tabulated when an adult hen was accompanied by one or more flightless ducklings of age-class I–III or by the presence of a hen actively engaged in distraction displays (i.e., a broody hen)

Canopy cover The more or less continuous cover of branches and foliage formed by the collective crowns of shrubs, forbs, and grasses. Also the top concealment over a nest

Cool-season grasses Grasses that initiate and do most of their growing during the cool seasons of the year when temperatures vary from 15° to 30° C (60° to 85° F); includes smooth brome, Kentucky bluegrass and needle-and-thread grass

Cover edge The zone where plant communities meet or where successional stages or vegetative conditions within plant communities come together

Cover height Generally, the average maximum height of leafy cover of grasses, forbs and shorter shrubs

Cropland Areas that are planted to grain or row crops, or that are plowed and left fallow. Usually these areas receive some tillage each year

Dabblers or dabbling ducks Mallard, gadwall, American wigeon, blue-winged teal, green-winged teal, northern shoveler, northern pintail and wood duck. These birds have surface dabbling feeding habits as opposed to divers

Depredation The art or instance of robbing, plundering, or laying waste to a nest or clutch

Divers or diving ducks Canvasback, red head, lesser scaup, ring-necked duck, and ruddy duck. These birds dive below the water surface to feed as opposed to dabblers

Duck pair A group of one or more adult ducks that were recognized as indicating a nesting pair. Indicated pairs were partitioned for final tabulation: segregated pairs and lone drakes were tabulated for both dabblers and divers, lone hens were tabulated only for divers and only when males were not nearby, and male groups and mixed groups of males and females were tabulated for groups up to five with the exception of northern shovelers and American wigeon for which only lone males and pairs are counted (Hammond 1969)

Emergent vegetation Plants rooted in soil with their lower portions submersed, but with most of their photosynthetic tissues above water, such as cattail or bulrush

Exposure days The number of days a clutch of eggs is under observation and vulnerable to loss to predators or other decimating factors

Full clutch Clutch size of incubated nests that have no history of destroyed or missing eggs

Grassland Areas vegetated with various mixtures of grasses, forbs, and short woody species

Grazed habitat An area that was purposely grazed with domestic livestock at some time during a calendar year

Hayland Areas that have been plowed and seeded to mixtures of grasses or legumes for forage production and that are hayed annually

Herbaceous plants Plants having little or no woody tissue. Portions of perennial herbaceous plants above ground die back each year and are replaced by new growth

Idled habitat An area that was not been burned, grazed, or cultivated during a calendar year and that has a continuous stand of the current year's plant growth or residual vegetation present

Lodged vegetation Vegetation, alive or dead, that has been knocked down by some force

Mayfield method for computing nest success A method that uses the interval during which a nest is under observation and exposed to decimating factors

Native prairie Natural grassland that has never been tilled and most of which is classified as mixed-grass prairie consisting of a mixture of short, medium and tall grasses and forbs

Nest A scrape or bowl containing one or more eggs. The terms "nest" and "clutch" are often used interchangeably in this and other duck nesting study reports. Only nests tended by hens (not destroyed or abandoned) when found are used to compute nest success by the methods described

Nest fate The success or failure of a nesting attempt

- **Abandoned** Intact clutches that are deserted by the hen. True abandonment rates are difficult to estimate because some untended clutches result from the death or injury of hens and some abandoned clutches are destroyed before their true fate can be determined. Abandoned clutches (other than those abandoned because of investigator disturbance on the day found) are combined with destroyed clutches to compute survival rates
- **Destroyed** A nest in which one or more eggs are missing or destroyed and none hatched
- **Fate unknown** The fate of the clutch was not determined because of inadequate evidence at the nest site or because the nest was not revisited
- **Nonviable** All eggs are infertile, addled, or contain dead embryos
- **Successful** One or more eggs hatched even if young are found dead at nest sites

Nest site Refers to the vegetation, soils, and other materials within a one meter circle centering on the nest scrape (bowl) and clutch

Nest site concealment Vegetation cover offering top (canopy) or side (surrounding) concealment of a nest

Nest success The probability that a nesting attempt will result in the production of one or more ducklings, as opposed to hen success—the probability that a hen will succeed in hatching at least one duckling in one or more nesting attempts

Nesting period The interval per year from the day the first egg was laid until the day the last egg was hatched for the population as a whole

Perennial A plant having a life span of more than two years

Predation Occurs when any organism kills another organism for food (e.g., a red fox kills a hen or eats some duck eggs)

Prescribed burning Deliberately burning a stand of grass or other vegetation to achieve management objectives

Residual cover The standing or lodged, dead portion of vegetation from the previous growing season

Seasonal wetland An area where surface water is present for extended periods, especially early in the growing season. In most years, surface water is absent by the end of the season. When surface water is absent, however, the water table is often near the land surface

Seeded cover Areas that are planted to mixtures of grasses and legumes for producing wildlife cover or for stabilizing soil under land retirement programs

Semi-permanent wetland An area where surface water persists throughout the growing season in most years. When surface water is absent, the water table is usually at or very near the land surface

Temporary wetland An area where surface water is present for brief periods during the growing season. The water table usually lies well below the soil surface for most of the year

Terminated nests Nests, successful or unsuccessful, no longer tended by a hen

Traditional method of computing nest success The number of nests in which one or more eggs hatched divided by the total number of nests of known fate that were found; reported as apparent nest success. Estimates by this method are almost always extremely biased

Upland nesting ducks Mallard, gadwall, American wigeon, blue-winged teal, green-winged teal, northern shoveler, northern pintail and lesser scaup. As opposed to those species which normally nest over water

Vegetation physiognomy A combination of the external appearance of vegetation, its vertical structure, and the life forms of its dominant taxa

Visual obstruction The 100% horizontal obstruction of the vegetation as read on a 5 cm-square cover pole from a distance of 4 m and a sighting height of 1 m

Warm-season grasses Grasses that do most of their growing during late spring and summer when temperatures reach or exceed 29° C; includes big bluestem, little bluestem, and switch grass

Wet basin A wetland was considered to be wet when a basin was at least 5% inundated and the water was 2.5 cm or more deep

Wetland complex A collection of wetlands of varying sizes, water depths, and plant communities, all in close proximity

A list of current *Resource Publications* follows.

166. Checklist of Vertebrates of the United States, the U.S. Territories, and Canada, by Richard C. Banks, Roy W. McDiarmid, and Alfred L. Gardner. 1987. 79 pp.
167. Field Guide to Wildlife Diseases. Vol. 1. General Field Procedures and Diseases of Migratory Birds, by Milton Friend, Cynthia J. Laitman, and Randy Stothard Kampen. 1987. 225 pp.
168. Mourning Dove Nesting: Seasonal Patterns and Effects of September Hunting, by Paul H. Geissler, David D. Dolton, Rebecca Field, Richard A. Coon, H. Franklin Percival, Don W. Hayne, Lawrence D. Soileau, Ronnie R. George, James H. Dunks, and S. Dwight Bunnell. 1987. 33 pp.
169. Saltcedar Control for Wildlife Habitat Improvement in the Southwestern United States, by Theodore A. Kerpez and Norman S. Smith. 1987. 16 pp.
170. Pesticide Use and Toxicology in Relation to Wildlife: Organophosphorus and Carbamate Compounds, by Gregory J. Smith. 1987. 171 pp.
171. Sand and Gravel Pits as Fish and Wildlife Habitat in the Southwest, by William J. Matter and R. William Mannan. 1988. 11 pp.
172. Satellite Telemetry: A New Tool for Wildlife Research and Management, by Steven G. Fancy, Larry F. Pank, David C. Douglas, Catherine H. Curby, Gerald W. Garner, Steven C. Amstrup, and Wayne L. Regelin. 1988. 54 pp.
173. Key to Acanthocephala Reported in Waterfowl, by Malcolm E. McDonald. 1988. 45 pp.
174. Obsolete English Names of North American Birds and Their Modern Equivalents, by Richard C. Banks. 9188. 37 pp.
175. Procedures for the Analysis of Band-recovery Data and User Instructions for Program MULT, by Michael J. Conroy, James E. Hines, and Byron K. Williams. 1989. 61 pp.
176. Sago Pondweed (*Potamogeton pectinatus* L.): A Literature Review, by Harold A. Kantrud. 1990. 89 pp.
177. Field Manual for the Investigation of Fish Kills, by Fred P. Meyer and Lee A. Barclay, editors. 1990. 120 pp.
178. Section 404 and Wetland Alterations in the Platte River Basin of Colorado, by Douglas N. Gladwin, Mary E. Jennings, James E. Roelle, and Duane A. Asherin. 1990. 19 pp.
179. Hydrology of the Middle Rio Grande from Velarde to Elephant Butte Reservoir, New Mexico, by Thomas F. Bullard and Stephen G. Wells. 1991. 51 pp.

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